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Revision of the Neotropical huntsman spider genus *Vindullus* Simon (Araneae, Sparassidae)

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Abstract. The huntsman spider genus *Vindullus* Simon 1880 (Araneae, Sparassidae) is revised. *Olios gracilipes* Taczanowski 1872 is transferred to the genus and recognized as a senior synonym of the type species, *Vindullus viridans* Simon 1880, for which the former male syntype was designated as a lectotype. *Vindullus kratochvili* Caporiacco 1955 is placed as *incertae sedis* and four new species are described: *Vindullus undulatus* new species, *Vindullus gibbosus* new species, both from Peru and *Vindullus angulatus* new species, from Colombia and Venezuela and *Vindullus concavus* new species from Brazil.

Keywords: Taxonomy, new species, transfer, redescription, South America

As is the case with several genera of the spider family Sparassidae, proposed by Simon between 1880 and 1897, the taxonomic history of the genus *Vindullus* Simon 1880 is quite confusing, even more than that of the recently revised *Macrinus* Simon 1887 (Rheims 2007). *Vindullus* was originally proposed by Simon (1880) to include *V. viridans* Simon, described from Tefé, Amazonas, Brazil. The genus remained monotypic until 1890 when *V. similis* was described from Guatemala by O. Pickard-Cambridge (1890). In 1897 Simon transferred *V. viridans* to *Sparassus* Walckenaer stating that the eye arrangement was not enough to justify the generic status. Nevertheless, he maintained *Vindullus* as a species group within which he described *Sparassus* (*Vindullus*) *guttipes* Simon from Natal, Oriental Africa. Pocock (1898) followed Simon's grouping and described *Sparassus* (*Vindullus*) *stictopus* from South Africa. Although Simon (1897) transferred the type species *V. viridans* to *Sparassus* and thus synonymized both genera there was no formal transfer of the remaining *Vindullus* species, *V. similis*, which was transferred to *Sparassus* by F.O. Pickard-Cambridge (1900).

A few years later Simon (1903) again transferred *V. viridans*, this time placing it in *Olios* Walckenaer. Once again, nothing was said about the species placed in the *Vindullus* group of *Sparassus*, which were only transferred to *Olios* in 1911 by Petrunkevitch.

The genus was implicitly revalidated by Caporiacco (1955), who described *Vindullus kratochvilli* Caporiacco 1955 based on a female from Rancho Grande, Aragua, Venezuela. Once again, nothing was said about either *S. similis*, *S. guttipes*, nor *S. stictopus*, which to date remain in the genus *Olios*. Although these species are clearly not congeneric with the type species of *Olios*, *O. argelasius* (Walckenaer 1805), they cannot, at present, be placed in any other known genus of Sparassidae. None of the three species is congeneric with the type species of *Vindullus*. Thus, until the present study, the genus *Vindullus* was composed of only two species, *V. viridans* and *V. kratochvilli* (Platnick 2008).

In this study, a revision of the genus *Vindullus* is presented. The type species, *V. viridans*, is redescribed and *Olios gracilipes* Taczanowski 1872 is transferred to the genus. *Vindullus kratochvilli* Caporiacco 1955 is found not to be congeneric with the type species, *V. gracilipes*, and, thus, is placed as *incertae sedis* until further knowledge on the Neotropical Sparassidae fauna is attained.

METHODS

The material examined belongs to the following institutions (Abbreviation and curator in parenthesis): American Museum of Natural History, New York (AMNH, N.I. Platnick); Instituto Butantan, São Paulo (IBSP, A.D. Brescovit); Museu Paraense Emílio Goeldi, Belém (MPEG, A.B. Bonaldo); Museo de Historia Natural de la Universidad San Marcos, Lima (MUSM, D. Silva); Muséum National d'Histoire naturelle, Paris (NMHN, C. Rollard), Polish Academy of Science, Museum of the Institute of Zoology, Warsaw (MZPW, K.W. Tomaszewska, T. Huflejt); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto da Rocha).

Abbreviations used throughout the text are: ALE = anterior lateral eyes; ALS = anterior lateral spinnerets; AME = anterior median eyes; d = dorsal; p = prolateral; PLE = posterior lateral eyes; PLS = posterior lateral spinnerets; PME = posterior median eyes; PMS = posterior median spinnerets; r = retrolateral; RTA = retrolateral tibial apophysis; v = ventral. Measurements are given in millimeters. The epigynum was dissected and submerged in clove oil to study internal structures. Micrographs were obtained with a JEOL (JSM 840A) scanning electron microscope from the "Laboratório de Microscopia Eletrônica do Departamento de Física Geral do Instituto de Física da Universidade de São Paulo (USP)." Coloration pattern was described based on preserved material.

TAXONOMY

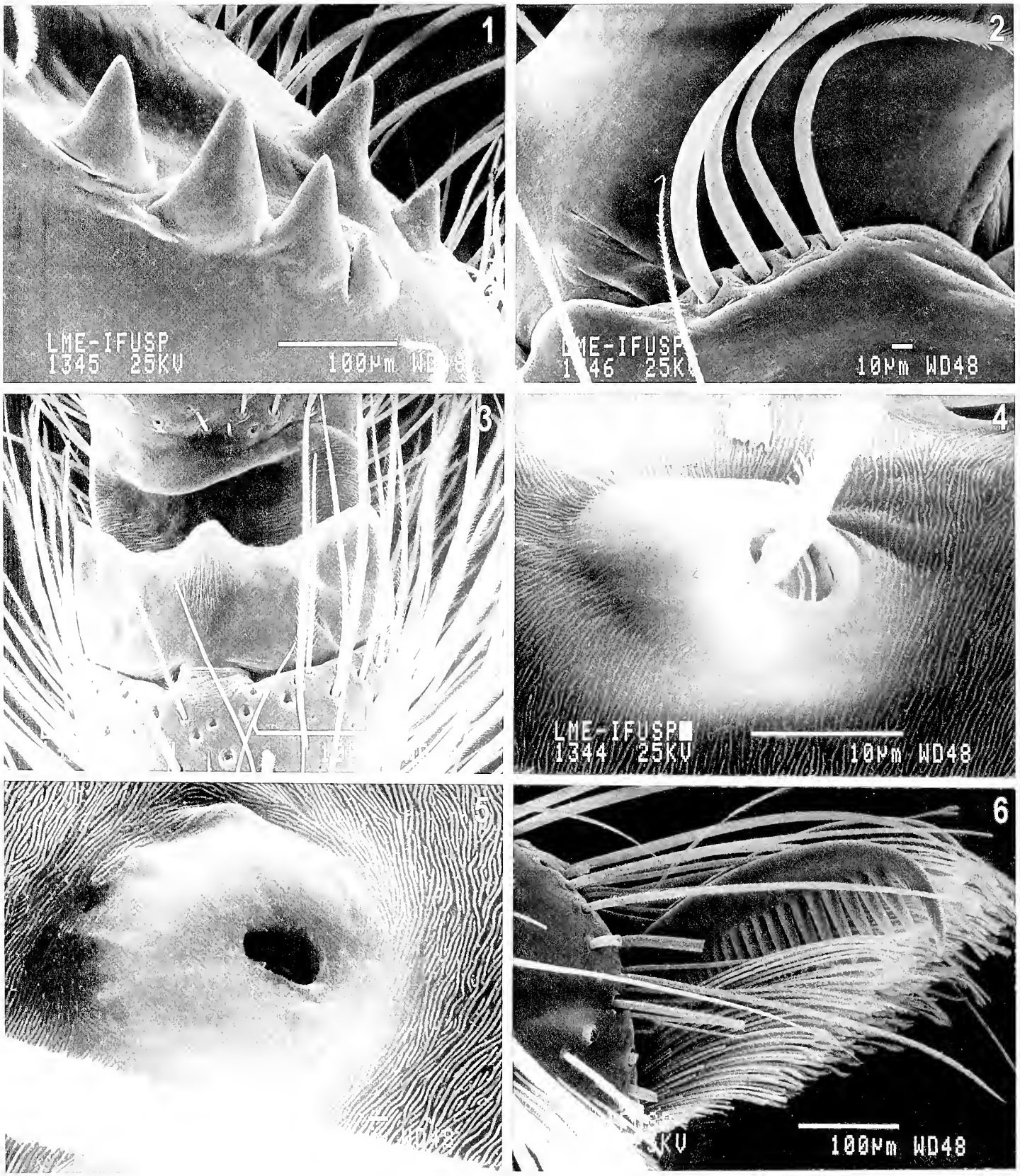
Family Sparassidae Bertkau 1872

Genus *Vindullus* Simon 1880

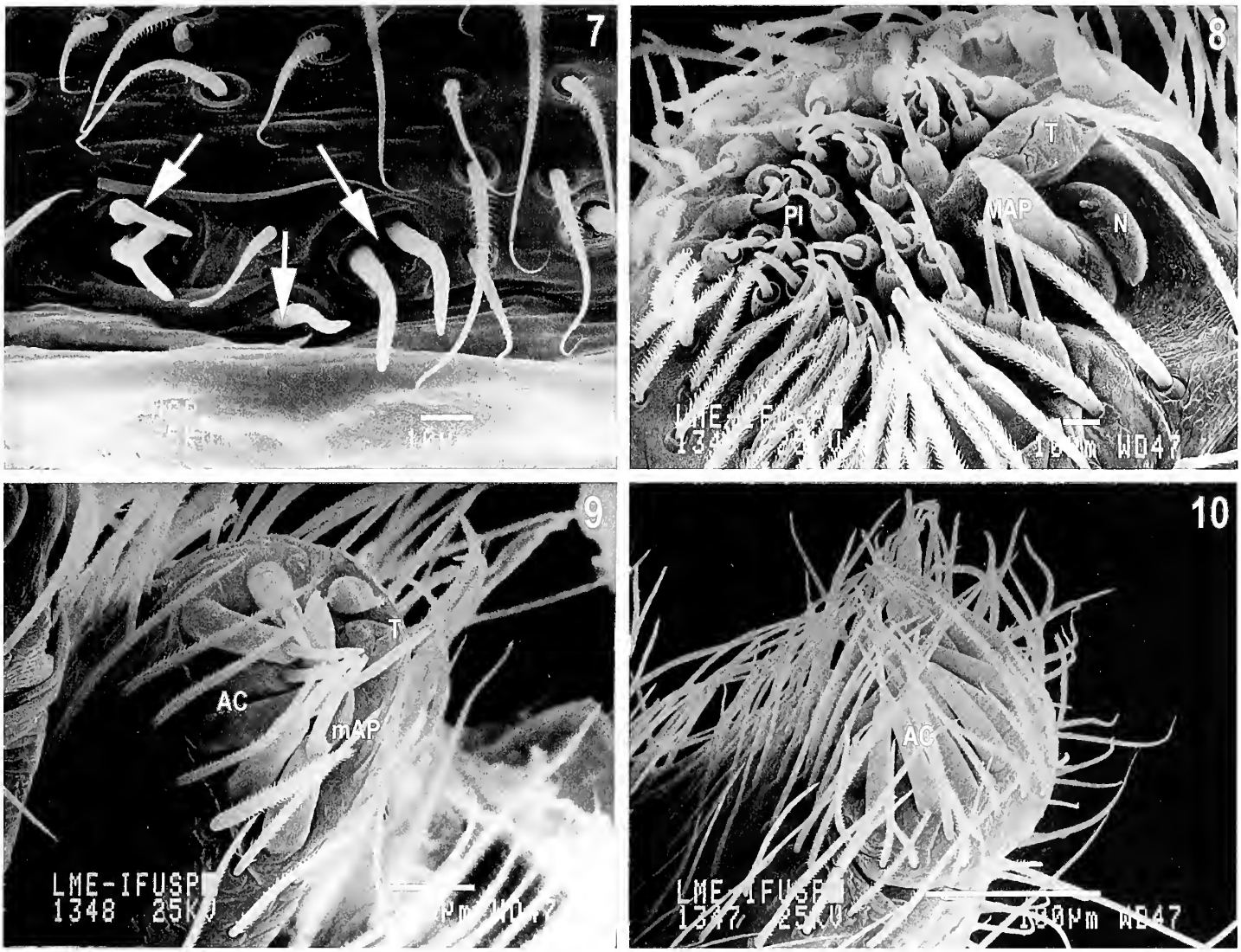
Vindullus Simon 1880:288; Caporiacco 1955:404; Platnick 2008.

Sparassus Walckenaer: Simon 1897:46 (in part).

Olios Walckenaer: Simon 1903:1025; Bonnet 1959:4797.



Figures 1–6. – *Vindullus angulatus* new species, male. 1. Cheliceral teeth, ventral view; 2. Chelicera, strong setae at base of fang, ventral view; 3. Distal metatarsus I, trilobate membrane, dorsal view; 4. Tarsus I, trichobothria, dorsal view; 5. Distal tarsus I, tarsal organ, dorsal view; 6. Distal tarsus I, claws, prolateral view.



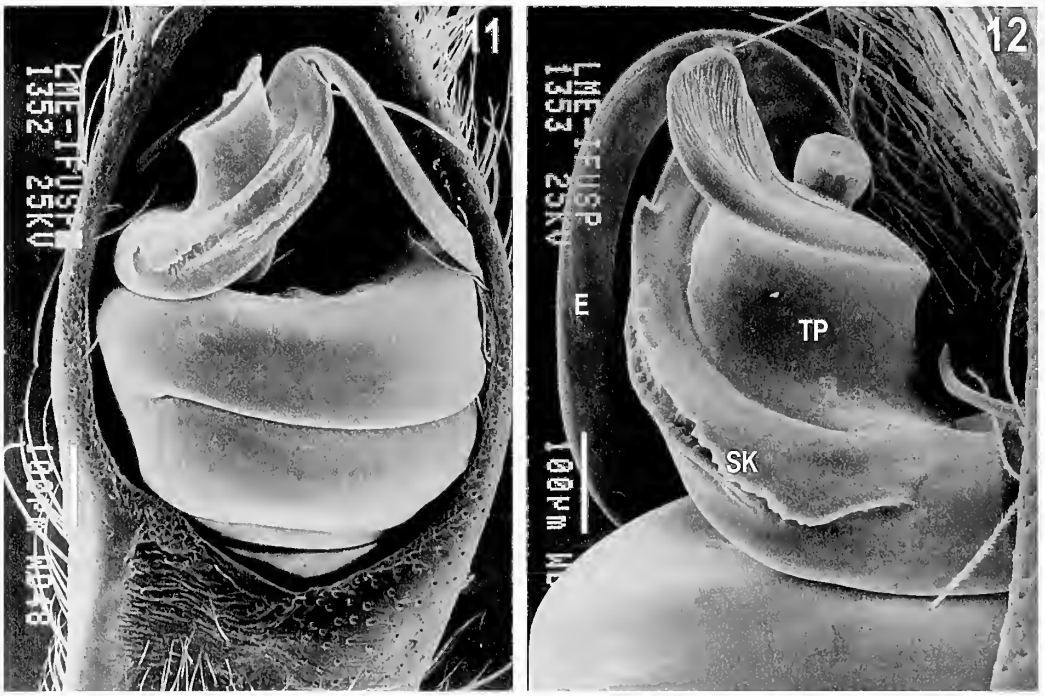
Figures 7–10.—*Vindullus angulatus* new species, male opisthosoma. 7. Epiandrous spigots, ventral view; 8. Anterior lateral spinnerets; 9. Anterior median spinnerets; 10. Posterior lateral spinnerets. AC = aciniform gland spigots; mAP = minor ampullate gland spigot; MAP = major ampullate gland spigot; N = nubin; PI = piriform gland spigots; T = tartipore.

Type species.—*Vindullus gracilipes* Tackzanowski 1872.

Relationships.—Evidence for the placement of *Vindullus* in Sparassinae includes the presence of only two promarginal teeth in the chelicerae, absence of intermarginal denticles, median hook of trilobate membrane as large as or slightly larger than lateral projections and a short-toothed female palpal claw (Jäger 1998). Within Sparassinae the genus seems to be closest to *Macrinus* Simon and *Nolavia* Kammerer with whom they share the presence of only two pairs of ventral spines on tibiae I–IV, the tegulum slightly spiraled perpendicularly to the main palpal axis, towards the tip of the cymbium (Figs. 16, 19, 22, 25, 31; Rheims 2007:figs. 22, 28, 34) and the female epigynum with simple, rounded lateral lobes partially covering the median septum (Fig. 28; Rheims 2007:figs. 24, 30, 36).

Diagnosis.—Species of the genus *Vindullus* are distinguished from the remaining Sparassinae genera by the presence of a distal laminar, triangular projection, bent at the tip and bearing a small hyaline protuberance (Figs. 12, 25, 31) and a serrated keel at the base of a filiform embolus, curved prolaterally dorsad, running a semicircle behind tegulum, appearing retrolaterally and pointing ventrad in the male palp (Figs. 16, 19, 22, 25, 31) and by the combination of a strongly sclerotized medium septum with a posterior, blind shaped atrium in the female epigynum (Figs. 27) and a strongly sclerotized duct system in the female vulva (Fig. 28).

Description.—Total length (males and females) 6.0–11.8. Prosoma as long as wide. Cephalic region slightly higher than thoracic region, gradually flattened posteriorly. Fovea conspicuous on posterior third of prosoma. Eyes arranged in two rows, the anterior recurved, AME similarly sized as ALE and farther apart from each other than from ALE. Posterior row straight, PME smaller than PLE and equidistant (Figs. 13, 14). Clypeus low, equal or slightly less than AME diameter. Chelicerae longer than wide with two promarginal teeth, the basal smaller and four or five retromarginal teeth, three subequal and most basal smaller (Fig. 1). Intermarginal denticles absent. Internal keel with 4–5 strong setae arranged in a row (Fig. 2). Labium rebordered, slightly wider than long. Endites longer than wide, slightly convergent, with dense



Figures 11, 12.—*Vindullus angulatus* new species, male. 10. Right palp, ventral view; 11. Left palp, retrolateral view. E = embolus; SK = serrated keel; TP = distal triangular projection.

scopulae on internal margin. Serrula with a single row of denticles. Sternum as long as wide, slightly projected between coxae IV. Legs laterigrade (2143). Leg spination in males: femora I–III: p1-1-1; d0-1-1; r1-1-1; femur IV: p1-1-1; d0-1-1; r 0-0-1; tibiae I–IV: p1-0-1; d0-0-1; r1-0-1; v2-2-0; metatarsi I–IV: p1-1-0; r1-1-0; v2-2-0. Leg spination in females as in males except femora II–IV: p0; r0-0-1; tibiae I–IV d0. Metatarsi I–IV with trilobate membrane with median hook slightly more developed than laterals (Fig. 3). Tarsi and distal half of metatarsi scopulate. Tarsal organ capsulate with oval opening, located dorsally at distal end of tarsi (Fig. 5). Trichobothria present on dorsal tibiae, metatarsi and tarsi, arranged in two parallel rows that converge into a single file on proximal half of tarsi and metatarsi. Trichobothrium with dorsal plate with few transverse grooves projected over a smooth basal plate (Fig. 4). Tarsi with pair of pectinate claws with 15 to 20 teeth and claw tufts (Fig. 6). Female pedipalp with single pectinate claw with 7–9 short and slightly curved teeth. Opisthosoma oval, longer than wide. Males with three or more clusters of epiandrous spigots (Fig. 7). Six spinnerets: ALS contiguous, conical and bi-segmented. Basal segment slightly elongate and cylindrical. Distal segment short and truncated with one major ampullate gland spigot, nubbin, tartipore and more than 20 piriform gland spigots (Fig. 8). AMS conical and short with one minor ampullate gland spigot, tartipore and approximately ten aciniform gland spigots (Fig. 9). PLS conical and bi-segmented. Basal segment slightly elongate. Distal segment short and truncated with 15–20 aciniform gland spigots (Fig. 10).

Palp: tibia short, slightly longer than half cymbium length, with one prolateral, one retrolateral and one dorsal strong spine. RTA short, not reaching alveolus, and conical (Figs. 17, 20, 23, 26, 32). Cymbium with strong dorsal scopula and rounded median alveolus. Tegulum slightly spiraled perpendicularly to the main palpal axis, towards the tip of the cymbium, with distal laminar, triangular projection, bent at the tip and bearing a small hyaline protuberance and a serrated keel at the base of a filiform embolus, curved prolaterally dorsad, running a semicircle behind tegulum, appearing retrolaterally and pointing ventrad in the male palp (Figs. 11, 12, 16, 19, 22, 25, 31). Conductor absent.

Epigynum: epigynal field divided into a pair of simple, rounded lateral lobes and a strongly sclerotized, heart-shaped medium septum, with a posterior blind ended atrium and pair of anterior copulatory openings (Fig. 27). Internally with strongly sclerotized duct system. Copulatory duct medially curved, bearing an anterior seminal receptacle. Spermathecae with a small cylindrical head and a larger, rounded base, from which emerges a long, medially twisted fertilization duct pointing laterad (Figs. 28, 29).

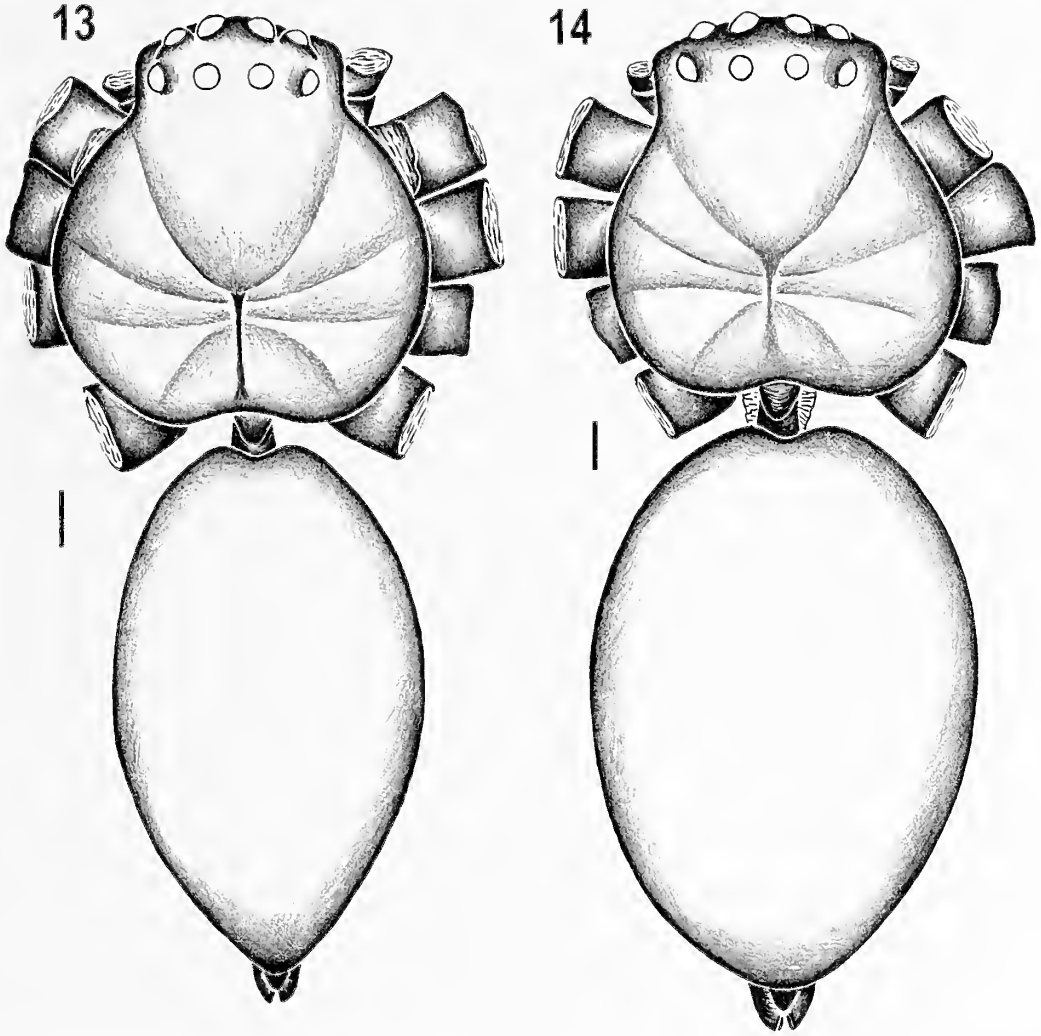
Distribution.—Known from northern South America (Colombia, Venezuela, Peru and northern Brazil).

Composition.—*Vindullus gracilipes* (Taczanowski) new combination, *Vindullus undulatus* new species, *Vindullus gibbosus* new species, *Vindullus angulatus* new species and *Vindullus concavus* new species.

Incertae sedis.—*Vindullus kratochvilli* Caporiacco 1955:406, fig. 58 (Male holotype from Rancho Grande, Aragua, Venezuela, deposited in MUCV 844, examined); Platnick 2008.

Vindullus gracilipes (Taczanowski 1872) new combination
Figs. 15–17

Olios gracilipes Taczanowski 1872:77 (Two male syntypes from French Guiana, Department de la Guyane, Cayenne [04°55′60″N; 52°19′60″W], R. Yelski leg., W.C. Taczanowski det., MZPW, examined). Mello-Leitão 1918:48, fig. 24; Platnick 2008.



Figures 13, 14.—*Vindullus angulatus* new species. 13. Male, habitus, dorsal view; 14. Female habitus, dorsal view. Scale lines: 0.5 mm.

Sparassus gracilipes: Keyserling 1880:241, pl.7, fig. 30.

Vindullus viridans Simon 1880:288 (Male, female and juvenile syntypes from Brazil, Amazonas, Tefé [03°22′S; 64°42′W], MNHN 1122, examined. Male lectotype herewith designated; female paralectotype does not belong to *Vindullus*). Caporiacco 1955:406; Platnick 2008. New synonymy.

Sparassus viridans: Simon 1897:36.

Olios viridans: Simon 1897:36. Petrunkevitch 1911:503; Mello-Leitão 1918:43; Bonnet 1958:3182.

Diagnosis.—Males of *V. gracilipes* Taczanowski 1872 are distinguished from those of the remaining species of the genus by the male palp with small distal area of the tegulum, only half as wide as the median area (Fig. 16), and by the RTA very slender and straight in retrolateral view (Fig. 17).

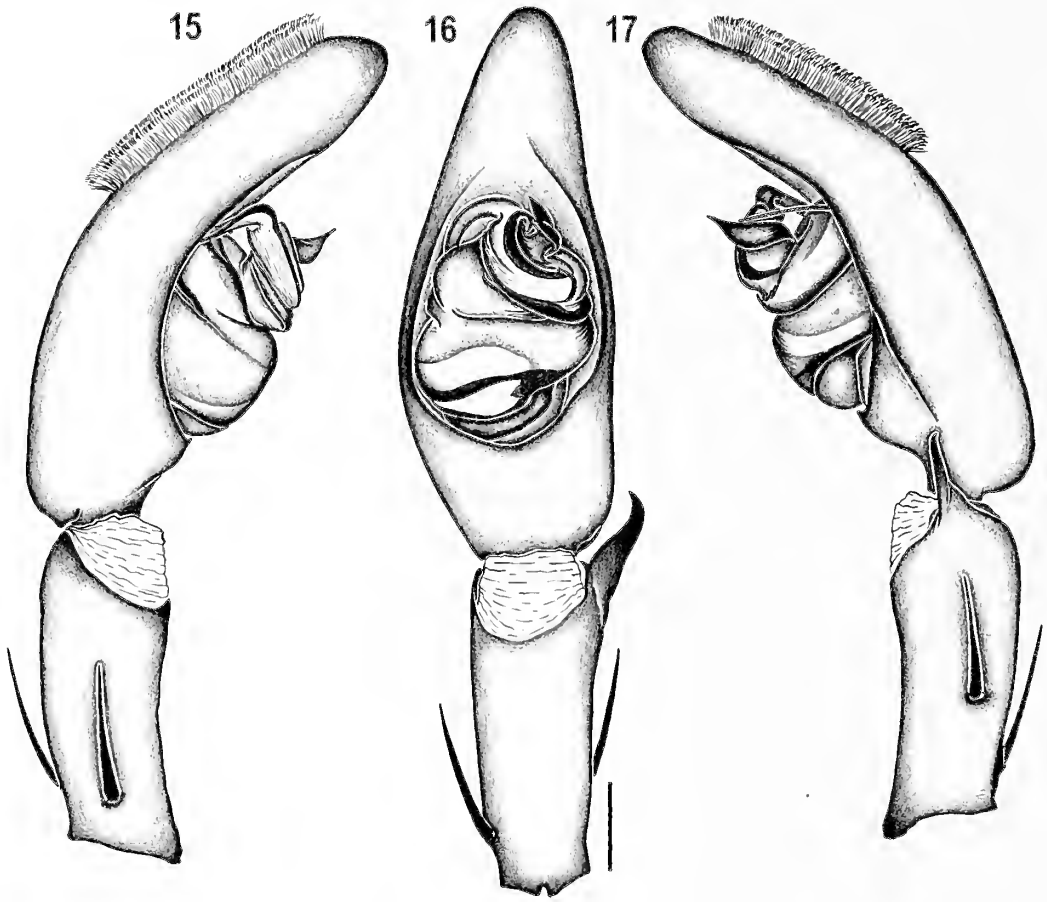
Description.—Male (MNHN 1122). Coloration: prosoma, chelicerae and legs pale orange; sternum pale yellow with darker margins; labium and endites pale orange, distally yellow; opisthosoma pale yellow. Total length 11.7. Prosoma 4.7 long, 4.2 wide. Opisthosoma 6.4 long, 3.6 wide. Eye diameters and interdistances: AME 0.44, ALE 0.32, PME 0.26, PLE 0.30, AME–AME 0.24, AME–ALE 0.04, PME–PME 0.38, PME–PLE 0.34, AME–PME 0.20, ALE–PLE 0.18. Leg measurements: I: absent; II: femur 9.2, patella 2.7, tibia 10.3, metatarsus 10.6, tarsus 2.2, total 35.0; III: 7.3, 2.1, 6.8, 6.8, 1.7, 24.7; IV: 8.3, 2.1, 7.6, 8.6, 1.9, 28.5. Spination follows the generic pattern. Palp: tibia with one prolateral, one retrolateral and one dorsal strong spine. RTA short, conical, slightly curved prolaterally at tip in ventral view and straight in retrolateral view. Subtegulum visible in ventral view (Fig. 16). Tegulum with small distal area. Distal triangular projection medially bent, with tip pointing ventrad in retrolateral view (Fig. 17). Conductor absent.

Female unknown.

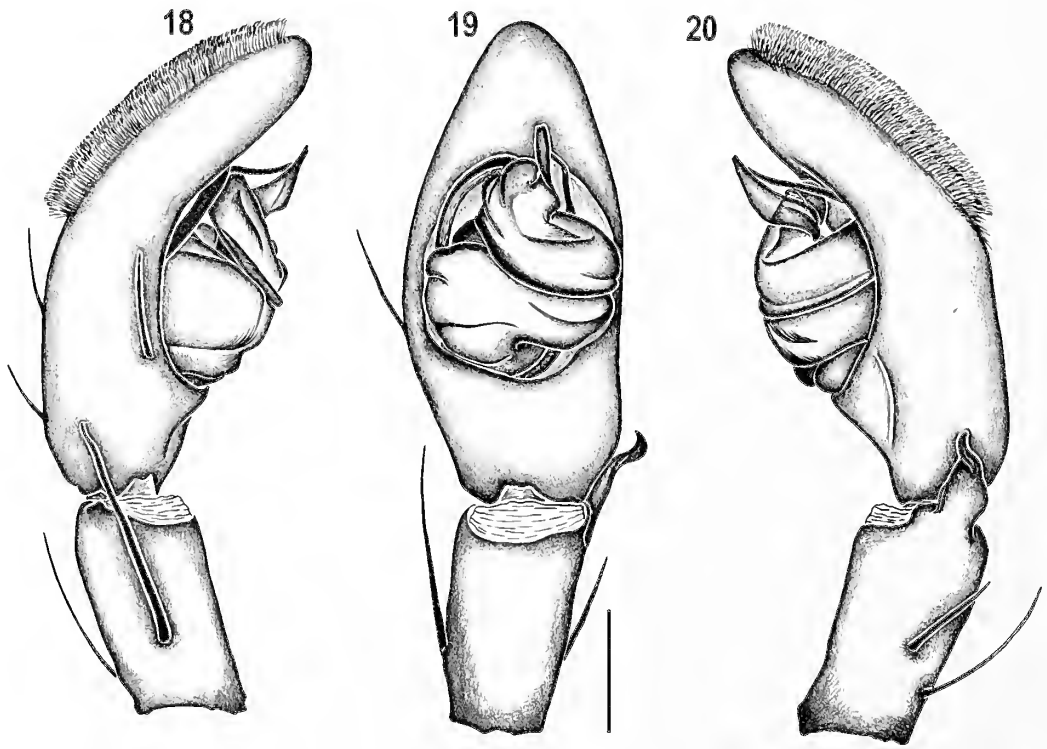
Distribution.—French Guiana (Cayenne; type locality), Brazil, (Amazonas: Tefé) (Fig. 33).

Vindullus undulatus new species
Figs. 18–20

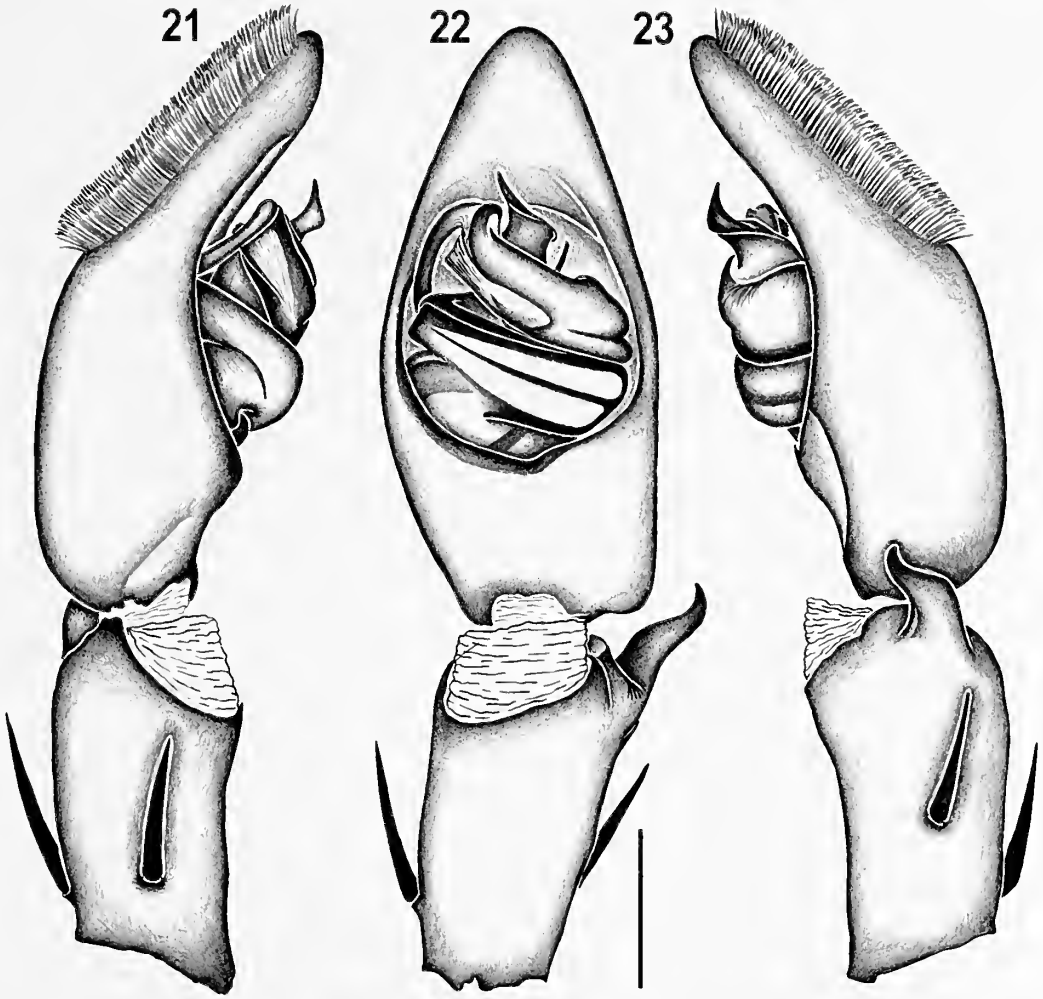
Type material.—Male holotype from Colombia, *Cesar*, Valledupar [10°28′37″N; 73°15′02″W], 22–24 May 1968, B. Malkin leg., deposited in AMNH. Paratypes: 4 males, 1 juvenile, 15 July 1968, (AMNH); 1 male, 1–3 September 1968 (AMNH); 1 male, 1 juvenile, 4–9 June 1968 (AMNH); 1 male, 15 July 1968 (IBSP 63813); all with the same locality and collector as holotype. 1 male, Venezuela, *Bolívar*, Puente Cocuizas, 70 km W. Bolívar [03°07′20″N; 62°32′59″W], 19 June–3 July 1987, S. & J. Peck leg. (AMNH).



Figures 15–17.—*Vindullus gracilipes* (Taczanowski), male, left palp. 15. Prolateral view; 16. Ventral view; 17. Retrolateral view. Scale line: 0.5 mm.



Figures 18–20.—*Vindullus undulatus* new species, male, left palp. 18. Prolateral view; 19. Ventral view; 20. Retrolateral view. Scale line: 0.5 mm.



Figures 21–23.—*Vindullus gibbosus* new species, male, left palp. 21. Prolateral view; 22. Ventral view; 23. Retrolateral view. Scale line: 0.5 mm.

Etymology.—The species name is derived from the Latin noun "unda" meaning "wave," referring to the undulated dorsal margin of the RTA in a retrolateral view; adjective.

Diagnosis.—Males of *Vindullus undulatus* new species resemble those of *Vindullus gibbosus* new species by male palp with distal area of the tegulum almost as wide as median area and by RTA with a wide base and narrow tip curved ventrad (Figs. 19, 20, 22, 23). They are distinguished by the RTA abruptly narrowed at tip (Fig. 20) and by the triangular projection very large and wide (Figs. 19, 20).

Description.—Male (AMNH). Coloration: prosoma orange, eye borders black; chelicerae orange, slightly darker than dorsal prosoma; labium brown, distally cream colored; endites cream colored, slightly darker at base; sternum orange with darker margins; legs and pedipalps orange; opisthosoma dorsally cream colored, faintly mottled light brown; spinnerets slightly darker than opisthosoma. Total length 6.5. Prosoma 2.9 long, 2.6 wide. Opisthosoma 3.5 long, 2.1 wide. Eye diameters and interdistances: AME 0.24, ALE 0.20, PME 0.18, PLE 0.20, AME–AME 0.16, AME–ALE 0.04, PME–PME 0.26, PME–PLE 0.22, AME–PME 0.22, ALE–PLE 0.14. Leg measurements: I: femur 3.6, patella 1.5, tibia 3.7, metatarsus 4.0, tarsus 1.1, total 13.9; II: 4.3, 1.7, 4.3, 4.6, 1.2, 16.1; III: 3.2, 1.2, 2.7, 2.8, 1.0, 10.9; IV: 3.7, 1.2, 3.2, 3.7, 1.1, 12.9. Spination follows the generic pattern. Palp: tibia with one prolateral, one retrolateral and one dorsal strong spine. RTA short, conical, wide at base and abruptly pointed at tip. Subtegulum visible in ventral view (Fig. 19). Tegulum with wide distal area. Distal triangular projection medially bent, with tip pointing towards tip of cymbium in retrolateral view (Fig. 20). Conductor absent.

Variation.—Nine males: total length 6.0–7.9; prosoma 2.8–3.6; femur I 3.6–5.6.

Female unknown.

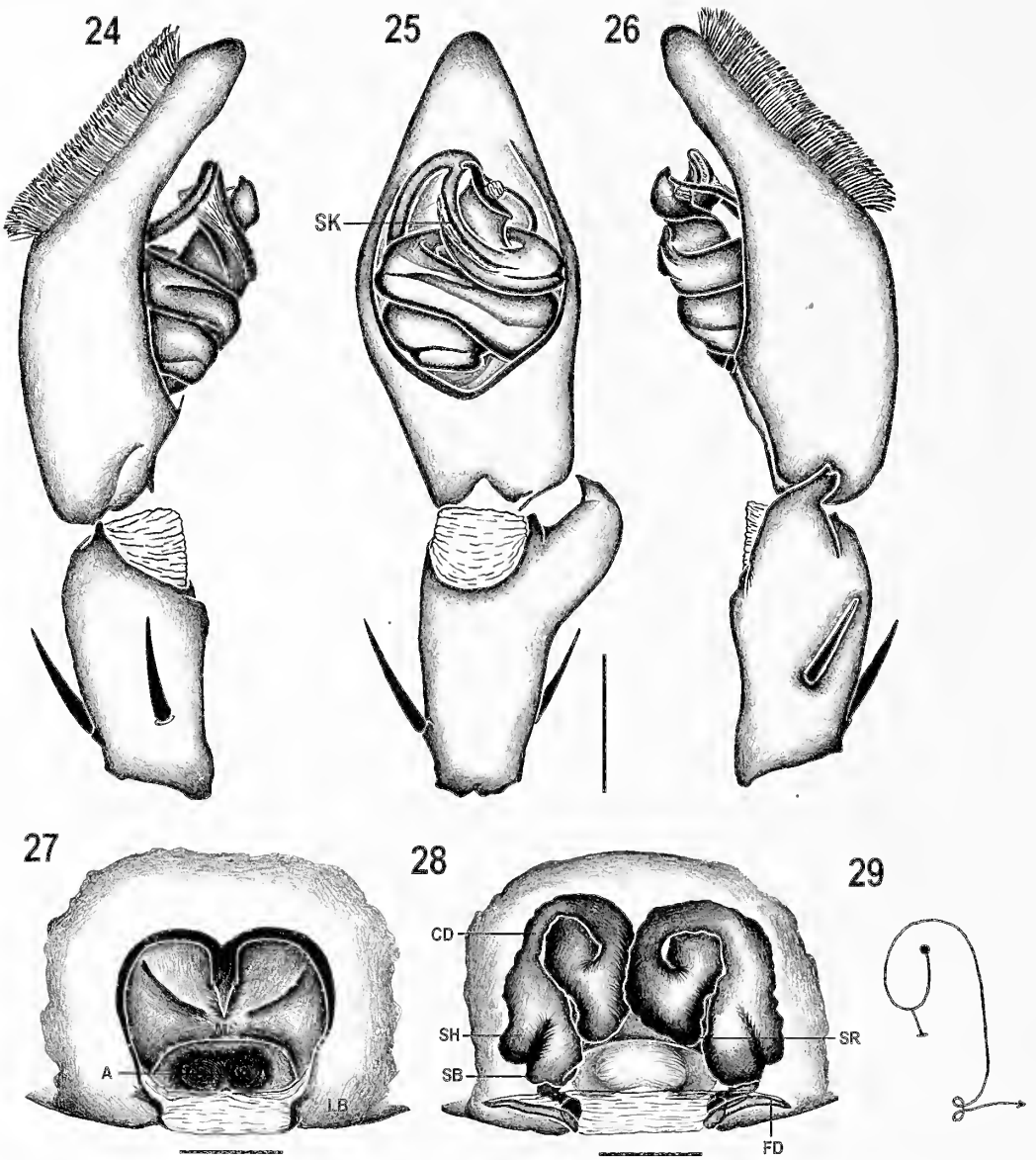
Distribution.—Northern South America: Colombia and Venezuela (Fig. 33).

Vindullus gibbosus new species
Figs. 21–23

Type material.—Holotype male from Peru, *San Martín*, Ekin, E. Tarapoto [06°30′05″S; 76°21′56″W], 9–21 March 1947, F. Woytkowski leg. (AMNH).

Etymology.—The species name is derived from the Latin noun "gibbus" meaning "hump," referring to the hump at the dorsal margin of the RTA in a retrolateral view; adjective.

Diagnosis.—Males of *Vindullus gibbosus* new species resemble those of *Vindullus undulatus* new species by the distal area of the tegulum almost as wide as the median area and by RTA



Figures 24–29.—*Vindullus angulatus* new species. 24–26. Male, left palp. 24. Prolateral view; 25. Ventral view; 26. Retrolateral view. 27–29. Female. 27. Epigynum, ventral view; 28. Epigynum, dorsal view; 29. Schematic course of internal duct system, dorsal view. A = atrium; CD = copulatory duct; FD = fertilization duct; LB = lateral lobe; MS = median septum; SB = spermathecae base; SH = spermathecae head; SR = seminal receptacle. Scale lines: 0.5 mm.

with a wide base and narrow tip curved ventrad (Figs. 19, 20, 22, 23). They are distinguished by the RTA gently curved ventrally and gradually pointed (Fig. 22) and the smaller triangular projection with a narrower tip (Figs. 21, 22).

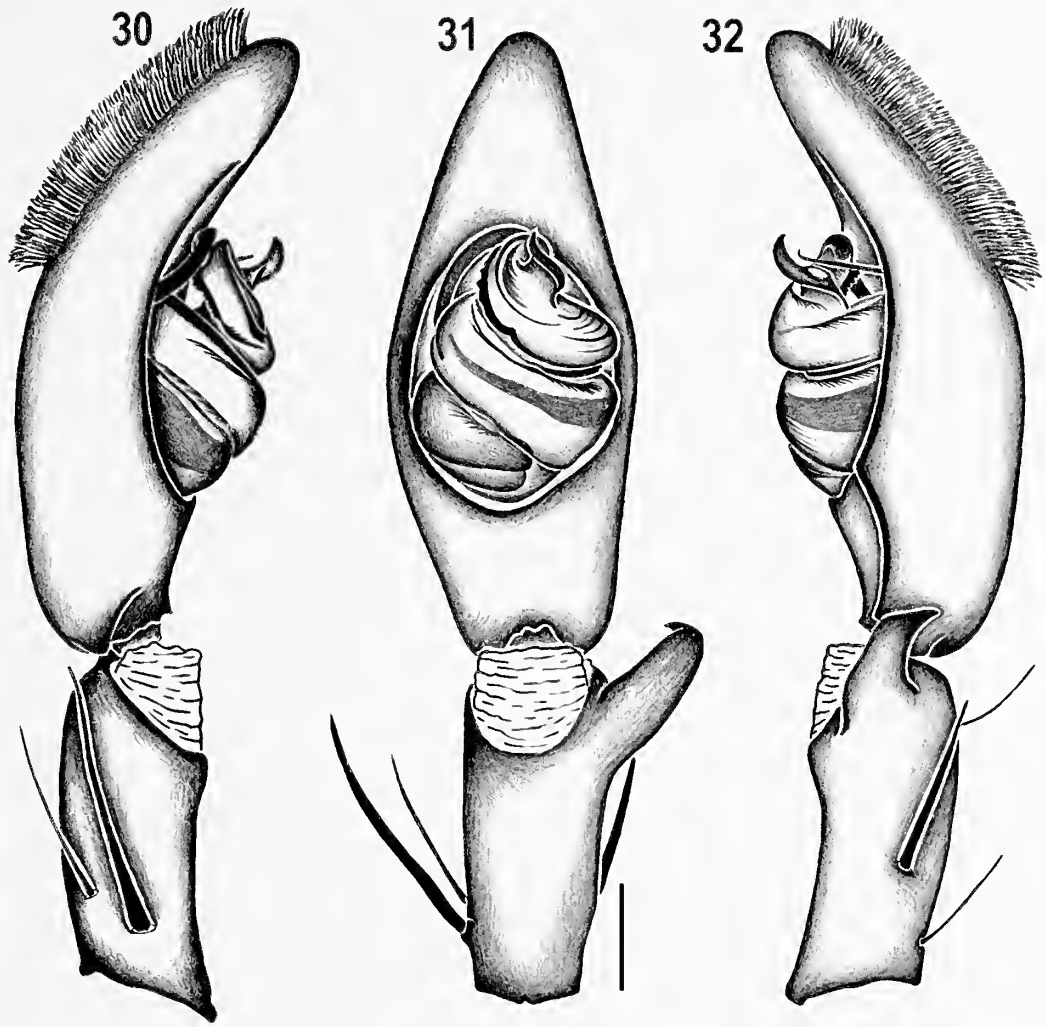
Description.—Male (holotype). Coloration: prosoma orange, slightly darker along fovea and striae; chelicerae orange with faint longitudinal brown stripe; labium dark orange, distally lighter; endites pale orange, distally cream colored; sternum orange with darker margins; legs and pedipalps orange; opisthosoma brownish gray, faintly variegated cream colored. Total length 9.0. Prosoma 4.3 long, 4.3 wide. Opisthosoma 4.7 long, 3.3 wide. Eye diameters and interdistances: AME 0.34, ALE 0.36, PME 0.24, PLE 0.26, AME–AME 0.22, AME–ALE 0.08, PME–PME 0.38, PME–PLE 0.38, AME–PME 0.28, ALE–PLE 0.20. Leg measurements: I: femur 6.8, patella 2.4, tibia 7.3, metatarsus 7.6, tarsus 2.0, total 26.1; II: 7.6, 2.5, 8.2, 8.5, 2.0, 28.8; III: 5.5, 1.8, 4.9, 5.0, 1.4, 18.6; IV: 6.2, 2.0, 5.6, 6.1, 1.5, 21.4. Spination follows the generic pattern. Palp: tibia with one prolateral, one retrolateral and one dorsal strong spine. RTA short, conical, wide at base and abruptly pointed at tip. Subtegulum visible in ventral view (Fig. 22). Tegulum with wide distal area. Distal triangular projection medially bent, with tip pointing towards tip of cymbium in retrolateral view (Fig. 23). Conductor absent.

Female unknown.

Distribution.—Known only from the type locality (Fig. 33).

Vindullus angulatus new species
Figs. 1–12; 24–29

Type material.—Holotype male from Peru, *Loreto*, Cocha Shinguito [05°08′S; 74°45′W], May–June 1990, T. Erwin & D.



Figures 30–32.—*Vindullus concavus* new species, male, left palp. 30. Prolateral view; 31. Ventral view; 32. Retrolateral view. Scale line: 0.5 mm.

Silva leg. (MUSM). Paratypes: 1 male, 1 female, same collection data as holotype (MUSM); 1 male, same collection data as holotype (IBSP 80705).

Etymology.—The species name is derived from the Latin adjective "angulatus, -a, -um," meaning "angled," referring to the almost right-angled indentation at the dorsal margin of the RTA in a retrolateral view (Fig. 29); adjective.

Diagnosis.—The males of *Vindullus angulatus* new species resemble those of *Vindullus concavus* new species by the RTA very wide and curved dorsally (Fig. 26, cf. Fig. 32) and by the very long and strong serrated keel at the base of the embolus in the male palp (Fig. 25, cf. Fig. 31). They are distinguished by the RTA abruptly bent dorsally and with a bifid tip (Fig. 26). The females are distinguished by the combination of a strongly sclerotized medium septum with a posterior, blind shaped atrium in the female epigynum (Fig. 27) and a strongly sclerotized internal duct system in the female vulva (Fig. 28).

Description.—Male (holotype). Coloration: dorsal shield of prosoma orange; chelicerae, legs, and pedipalps slightly lighter than dorsal prosoma; labium and endites pale orange, distally cream colored; sternum pale yellow with darker margins; opisthosoma brownish gray. Total length 9.3. Prosoma 3.7 long, 3.4 wide. Opisthosoma: 5.2 long, 2.8 wide. Eye diameters and interdistances: AME 0.30, ALE 0.28, PME 0.22, PLE 0.26, AME–AME 0.20, AME–ALE 0.06, PME–PME 0.28, PME–PLE 0.26, AME–PME 0.24, ALE–PLE 0.16. Leg measurements: I: femur 6.2, patella 2.0, tibia 6.6, metatarsus 7.2, tarsus 1.7, total 23.7; II: 7.1, 2.0, 7.4, 7.9, 1.7, 26.1; III: 4.9, 1.6, 4.5, 4.5, 1.3, 16.8; IV: 5.6, 1.7, 5.2, 5.7, 1.3, 19.5. Leg spination follows the generic pattern. Palp: tibia with one prolateral, one retrolateral and one dorsal strong spine. RTA short, conical, wide at base, dorsally curved and bifid at tip (Fig. 26). Subtegulum visible in ventral view (Fig. 25). Tegulum with wide distal area and strong serrated projection at embolus base. Distal triangular projection medially bent, with tip pointing towards tip of cymbium in retrolateral view (Fig. 26). Conductor absent.

Female (paratype). Coloration as in male. Total length 11.8. Prosoma 4.3 long, 4.3 wide. Opisthosoma 7.2 long, 5.0 wide. Eye diameters and interdistances: AME 0.34, ALE 0.36, PME 0.24, PLE 0.32, AME–AME 0.30, AME–ALE 0.06, PME–PME 0.40, PME–PLE 0.44, AME–PME 0.30, ALE–PLE 0.24. Leg measurements: I: femur 5.6, patella 2.2, tibia 5.4, metatarsus 5.7, tarsus 1.5, total 20.4;

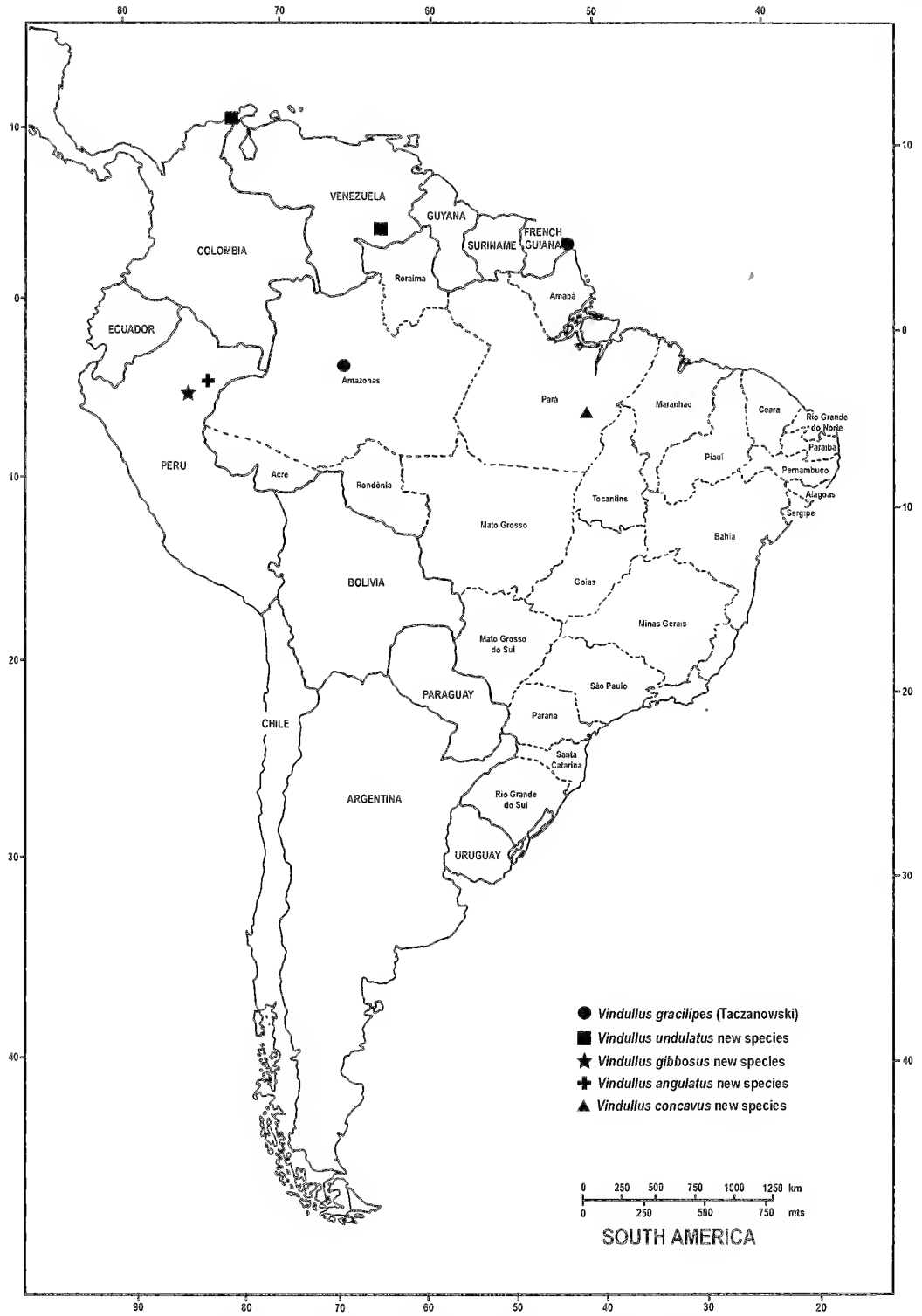


Figure 33.—Distribution map showing records of *Vindullus* spp.

II: 6.3, 2.4, 6.0, 6.1, 1.5, 22.3; III: 4.5, 1.8, 3.8, 3.7, 1.3, 15.1; IV: 5.1, 1.9, 4.5, 4.6, 1.2, 17.3. Spination follows the generic pattern. Epigynum: epigynal field divided into a pair of simple, rounded lateral borders and a strongly sclerotized, heart-shaped medium septum, with a posterior blind ended atrium and pair of anterior copulatory openings (Fig. 27). Internally with strongly sclerotized duct system. Copulatory duct medially curved, bearing an anterior seminal receptacle. Spermathecae with a small cylindrical head and a larger, rounded base, from which emerges a long, medially twisted fertilization duct pointing laterad (Figs. 28–29).

Variation.—Three males: total length 8.6–9.3; prosoma 3.5–4.0; femur I 6.0–6.8.

Distribution.—Known only from the type locality (Fig.33).

Vindullus concavus new species
Figs. 30–32

Type material.—Male holotype from Brazil, *Pará*, Rio Tocantins (west bank) Acampamento Barragem, 20 June 1984, H.A. Nteto leg., deposited in MPEG.

Etymology.—The species name is derived from the Latin adjective "concavus, -a, -um" meaning "arched inward," referring to the concave dorsal margin of the RTA in a retrolateral view; adjective.

Diagnosis.—The males of *Vindullus concavus* new species resemble those of *Vindullus angulatus* new species by RTA very wide and curved dorsally (Fig. 32, cf. Fig. 26) and by very long and strong serrated keel at the base of the embolus in the male palp (Fig. 31, cf. Fig. 25). They are distinguished by the gently curved RTA with a pointed tip (Fig. 32).

Description.—Male (MPEG). Coloration: prosoma orange, slightly darker at cephalic area and along fovea; chelicerae, legs, and pedipalps orange; sternum pale yellow with slightly darker margins; labium and endites pale yellow; opisthosoma whitish gray with conspicuous, cream colored cardiac impression. Total length 9.2. Prosoma 3.9 long, 3.5 wide. Opisthosoma 5.1 long, 3.1 wide. Eye diameters and interdistances: AME 0.34, ALE 0.28, PME 0.24, PLE 0.28, AME–AME 0.22, AME–ALE 0.02, PME–PME 0.28, PME–PLE 0.26, AME–PME 0.30, ALE–PLE 0.18. Leg measurements and interdistances: I: absent; II: femur 8.5, patella 2.5, tibia 8.7, metatarsus 9.7, tarsus 2.0, total 31.4; III: 6.1, 2.0, 5.5, 5.9, 1.5, 21.0; IV: 6.9, 2.0, 6.3, 7.2, 1.6, 24.0. Leg spination follows the generie pattern. Palp: tibia with one prolateral, one retrolateral and one dorsal strong spine. RTA short, conical, wide at base, and dorsally curved (Fig. 31). Subtegulum visible in ventral view (Fig. 31). Tegulum with wide distal area and strong serrated projection at embolus base (Fig. 30). Distal triangular projection medially bent, with tip pointing towards tip of cymbium in retrolateral view (Fig. 32). Conductor absent.

Female unknown.

Distribution.—Only known from the type locality (Fig. 33).

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Comb-hairs on the fourth tarsi in pholcid spiders (Araneae, Pholcidae)

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Abstract. Comb-hairs on the fourth tarsi of males and females are a classical theridioid character, but they also occur in pholcids. Previous studies on *Pholcus phalangioides* (Fuesslin 1775) have shown that in this species the comb-hairs function in the context of sticky silk wrap attack just as in theridiids. Here we investigate pholcid comb-hairs in a comparative way, studying the tarsal hairs of representatives of 42 pholcid genera with the SEM. We found two principal morphologies, a simple and a complex type of comb-hair. We found two principal types of comb-hair distribution on the tarsus: in distal patches or in ventral rows, but intermediate types also occur. Character mapping suggests that simple comb-hairs are derived from complex ones, and that distal patches are plesiomorphic, ventral rows derived. We speculate that pholcid comb-hairs may be derived from hairs (the "accessory claws") that grasp silk in functional correlation with the median claw. In a female shock-frozen during wrap attack, the silk line passed through the notch of a comb-hair, but several functional details (silk grasping and releasing, function of different hair branches) remain unanswered.

Keywords: Sticky silk wrap attack, silk manipulation, morphology

Comb-hairs on the fourth tarsi are a classic character of theridioids (Theridiidae and Nesticidae). In these spiders, comb-hairs are thought to function in the context of sticky silk wrap attack ("ss-wrap"). In contrast to other spiders, theridiids and nesticids wrap prey with sticky silk rather than with dry silk (e.g., Nielsen 1932; Kirchner & Kullmann 1972; Carico 1978; Coddington 1986; Whitehouse 1987; Forster et al. 1990; Griswold et al. 1998). The fact that this is done with the fourth tarsi strongly suggests this functional interpretation of comb-hairs even though the exact mechanics of the interactions between comb-hair and silk remain unknown.

Other than theridioids, only the distantly related Pholcidae are known to use sticky silk during wrap attack, at least during the early phases of wrapping (Eberhard 1992; Japyassú & Macagnan 2004). The convergence goes even further in that pholcids, too, use their fourth legs to wrap prey (e.g., Jackson & Brassington 1987; Kirchner & Opderbeck 1990; Japyassú & Macagnan 2004), and recent studies have shown that several genera within the family have comb-hairs on the fourth tarsi that show considerable similarity to those of certain theridiid taxa (*Belisana*: Huber 2005a; *Spermophora*: Huber 2005b; *Carapoia*: Huber 2005c; *Metagonia*: Huber et al. 2005; *Leptopholcus*: Huber & Wunderlich 2006).

This striking convergence strengthens the idea that the comb-hairs are directly correlated with the manipulation of sticky silk. However, just as in theridiids, the details of interaction remain unknown. Previously, only the study by Kirchner & Opderbeck (1990) has looked in some detail at the comb-hairs in *Pholcus phalangioides* (Fuesslin 1775). These authors photographed the spider during wrapping, showing that the fourth tarsus indeed holds the silk line, and it is quite evident from their figure 5 that it is not the tarsus tip (the claws) that grasp the line but the more proximal section.

The present study is the first to give a wide comparative overview of pholcid comb-hairs that were discovered long ago (Lebert 1874) in *P. phalangioides* but that were until recently never searched for in other pholcids. A few recent studies (above) have shown variation within the family, both in hair structure and position, but the data were too scarce to allow a meaningful evolutionary interpretation. By mapping details of comb-hair morphology on cladograms derived from other morphological and from molecular data we trace the evolution of comb-hairs in Pholcidae.

METHODS

We studied the fourth tarsal hairs of representatives of 42 pholcid genera and of three outgroups (Table 1) using SEM (Hitachi S-2460). In addition, in some species we scanned all tarsi of both males and females. In *P. phalangioides* we also studied young juveniles (~2.5 mm total body length). For character mapping we used a composite cladogram derived from recent morphological and molecular work on pholcid phylogeny (Huber 2000, 2001, 2003a, b, c, 2005a, b; Bruvo-Madarić et al. 2005; Huber & El Hennawy 2007; Astrin et al. 2007; B.A. Huber unpublished data on *Pholcus* and close relatives). In order to see the details of hair-silk interaction, we freeze-fixed four *P. phalangioides* and two *Psilochorus simoni* (Berland 1911) specimens during wrap attack using a freezing spray (Reparil® Ice-Spray Madaus). Specimens were immediately transferred to 80% ethanol at −20° C and kept at this temperature for one week. The fourth legs were then detached from the spider and studied with the SEM. Vouchers of all species studied and SEM stubs are deposited at the Alexander Koenig Research Museum of Zoology, Bonn.

RESULTS

Except for the two Old World ninetines we studied (*Ninetis*, *Nita*), we found comb-hairs in all pholcid species. In those species where all tarsi were examined, comb-hairs occurred only on the fourth tarsi. We found no evidence for sexual dimorphism. Comb-hairs were also present in *P. phalangioides* juveniles. There was considerable variation both in comb-hair morphology and distribution on the fourth tarsi.

Comb-hair morphology.—We found two main types of comb-hairs, each one widely distributed among genera, and a few deviant types restricted to single species. We call the two main types the "*Pholcus*-type" and the "*Belisana*-type." The

Table 1.—Taxa studied, sexes studied, and previous publications showing pholcid tarsal comb-hairs. Asterisks indicate species for which all tarsi were examined.

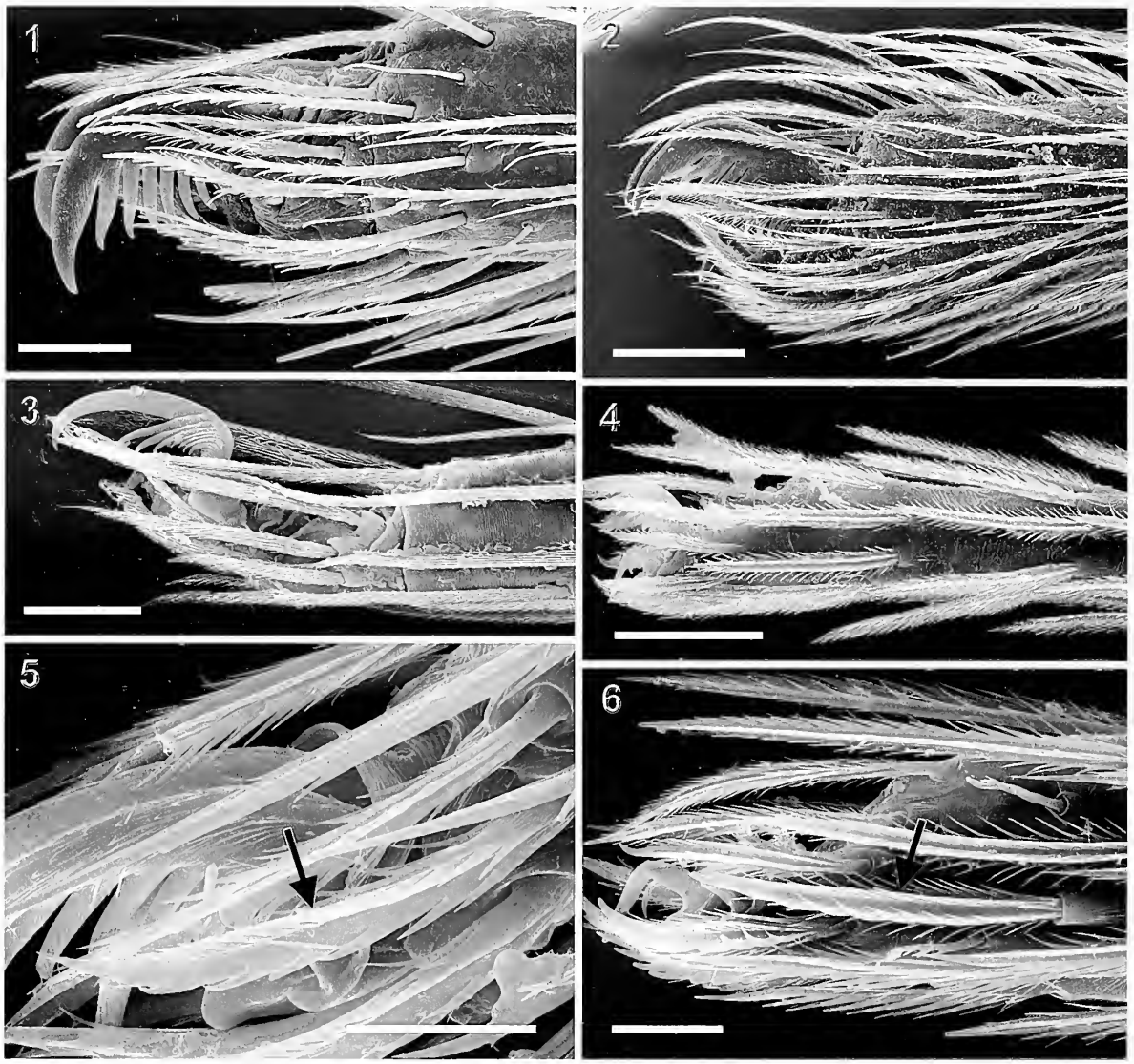
Species	m/f	Previous publications
Outgroups		
Diguetia signata Gertsch 1958	f	
Ochyrocera sp. (Costa Rica, Escazú)	m	
Plectreurys tristis Simon 1893	f	
Ninetinae		
Aucana kaala Huber 2000	m	
Ibotyporanga naideae Mello-Leitão 1944	f	
* *Ninetis toliara* Huber & El Hennawy 2007	m	
* *Nita elsaff* Huber & El Hennawy 2007	m	
Pholcophora americana Banks 1896	m/f	
New World Clade		
Anopsicus chickeringi Gertsch 1982	m	
Carapoia spp.	f	Huber 2005c
Chibchea ika Huber 2000	m	
Ciboneya autraia Huber & Pérez 2001	m	
Mecolaesthus longissimus Simon 1893	m	
Mesabolivar eberhardi Huber 2000	m	
Mesabolivar sp. ("Brazil 7")	m	
Mesabolivar yuruani (Huber 2000)	f	
* *Modisimus guatuso* Huber 1998	m/f	
Priscula sp. ("Venezuela 1")	m	
Tainonia sp. ("samana")	m/f	
Holocnemines I		
Artema atlanta Walckenaer 1837	f	
Holocnemimus piritarsis Berland 1942	f	
Physocyclus globosus (Taczanowski 1874)	f	
Trichocyclus nullarbor Huber 2001	f	
Holocnemines II		
Crossopriza lyoni (Blackwall 1867)	f	
Holocnemus pluchei (Scopoli 1763)	m	
Hoplopholcus minotaurus Senglet 1971	f	
* *Smeringopina pulchra* (Millot 1941)	f	
Smeringopina sp. ("USNM 9")	f	
Smeringopus natalensis Lawrence 1947	m	
Pholcinae – 'Basal' Taxa		
* *Belisana* spp.	m/f	Huber 2005a
Buitinga asax Huber 2003	m	
Khorata khammouan Huber 2005	m/f	
Metagonia conica (Simon 1893)	m	
Metagonia reventazona Huber 1997	m	
Metagonia spp.	m/f	Huber et al. 2005
Nyikoa limbe Huber 2007	m/f	
Paramicromerys scharffi Huber 2003	f	
Quamtana bonamanzi Huber 2003	f	
Spermophora senoculata (Dugès 1836)	f	
Spermophora usambara Huber 2003	m	
Spermophora spp.	f	Huber 2005b
Spermophorides cuneata (Wunderlich 1987)	m	
Spermophorides elevata (Simon 1873)	m	
Zatavua vohiparara Huber 2003	f	
Pholcinae – *Pholcus* and Close Relatives		
Calapnita phyllicola Deeleman-Reinhold 1986	m	
Leptopholcus spp. (Dom. Rep.)	m/f	Huber & Wunderlich 2006
Leptopholcus hispaniola Huber 2000	m/f	
Micromerys daviesae Deeleman-Reinhold 1986	m	
Micropholcus fauroti (Simon 1887)	m	
Ossinissa justoi (Wunderlich 1992)	f	
Panjange mirabilis Deeleman-Reinhold 1986	f	
Pehrforsskalia conopyga Deeleman-Reinhold & van Harten 2001	m	
* *Pholcus opiliounoides* (Schrank 1781)	m/f	
Pholcus phalangioides (Fuesslin 1775)		Kirchner & Opderbeck 1990
Uthina luzonica Simon 1893	f	

Pholcus-type of comb-hair is simple; it consists basically of a main shaft that is distally slightly curved or hooked and about four to six hooked branches directed to the same side (Figs. 25–31). The *Belisana*-type of comb-hair is considerably more complex. It consists of a main shaft with three distinctive rows of branches (Figs. 5–24): a ventral (with respect to the tarsus) row of about 6–12 curved (or slightly hooked) branches, a dorsal row of about 6–10 fairly straight and usually thin branches, and between these rows another row of about 10–30 short straight branches. Deviant types of hairs occur in *Artema atlanta* Walckenaer 1837 (*Belisana*-type but unusually strong branches in the median row, Figs. 17, 18), *Priscula* sp. (only two rows of branches visible in lateral view, Fig. 11), and some *Spermophora* and Pacific *Belisana* species (e.g., *B. airai* Huber 2005, *B. fiji* Huber 2005; high number of ventral branches very close together, Fig. 24; see also figs. 477, 639 in Huber 2005a).

Comb-hair length ranges from about 40 to 160 µm for both types and seems to be closely related to the overall size of the spider. In *P. phalangioides* spiderlings, comb-hair length was about 45–50 µm, in adults 90–105 µm. Interestingly, the short comb-hairs in juveniles tended to have more rather than fewer branches (4–5 versus 3–4 in adults).

Comb-hair distribution.—Pholcid comb-hairs show two main types of distribution on the tarsus. They are either limited to patches of hairs distally on the tarsus (Figs. 5–12) or they are aligned ventrally (or slightly prolaterally) in a single row (Figs. 19–30). In the first case, patches of hairs occur both on the prolateral and retrolateral sides, but the prolateral patch is more developed, both in terms of number of hairs (usually about 3–6) and in the distinctiveness of the comb-hairs themselves. The retrolateral patch may consist of no more than one or two modified hairs. Additional (apparently intermediate) types of distribution were found in certain "holocnemines" where the prolateral patches of hairs extend farther towards the basis of the tarsus, in some cases resulting in two ventral-prolateral rows (Fig. 14) of hairs spread over almost the entire length of the tarsus.

Character mapping and optimization.—Character mapping on the cladogram in Fig. 32 allows the reconstruction of the evolutionary simplification of comb-hair morphology within Pholcidae. The *Pholcus*-type of comb-hair evolved once within Pholcinae, supporting a group of genera closely related to *Pholcus*. The origin of the plesiomorphic *Belisana*-type of hair



Figures 1–6.—Hairs on tarsus 4 tip, outgroups and ninetines. 1. *Diguetia signata*, female right tarsus 4, prolateral; 2. *Plectreurys tristis*, female right tarsus 4, prolateral; 3. *Ochyrocera* sp., male left tarsus 4, retrolateral; 4, *Nita elsaff*, male left tarsus 4, retrolateral; 5. *Ibotyporanga naideae*, female right tarsus 4, prolateral; 6. *Pholcophora americana*, female right tarsus 4, prolateral (main claws missing). Arrows point to comb-hairs. Scale lines: 20 μm (3, 5, 6), 40 μm (4), 60 μm (1), 200 μm (2).

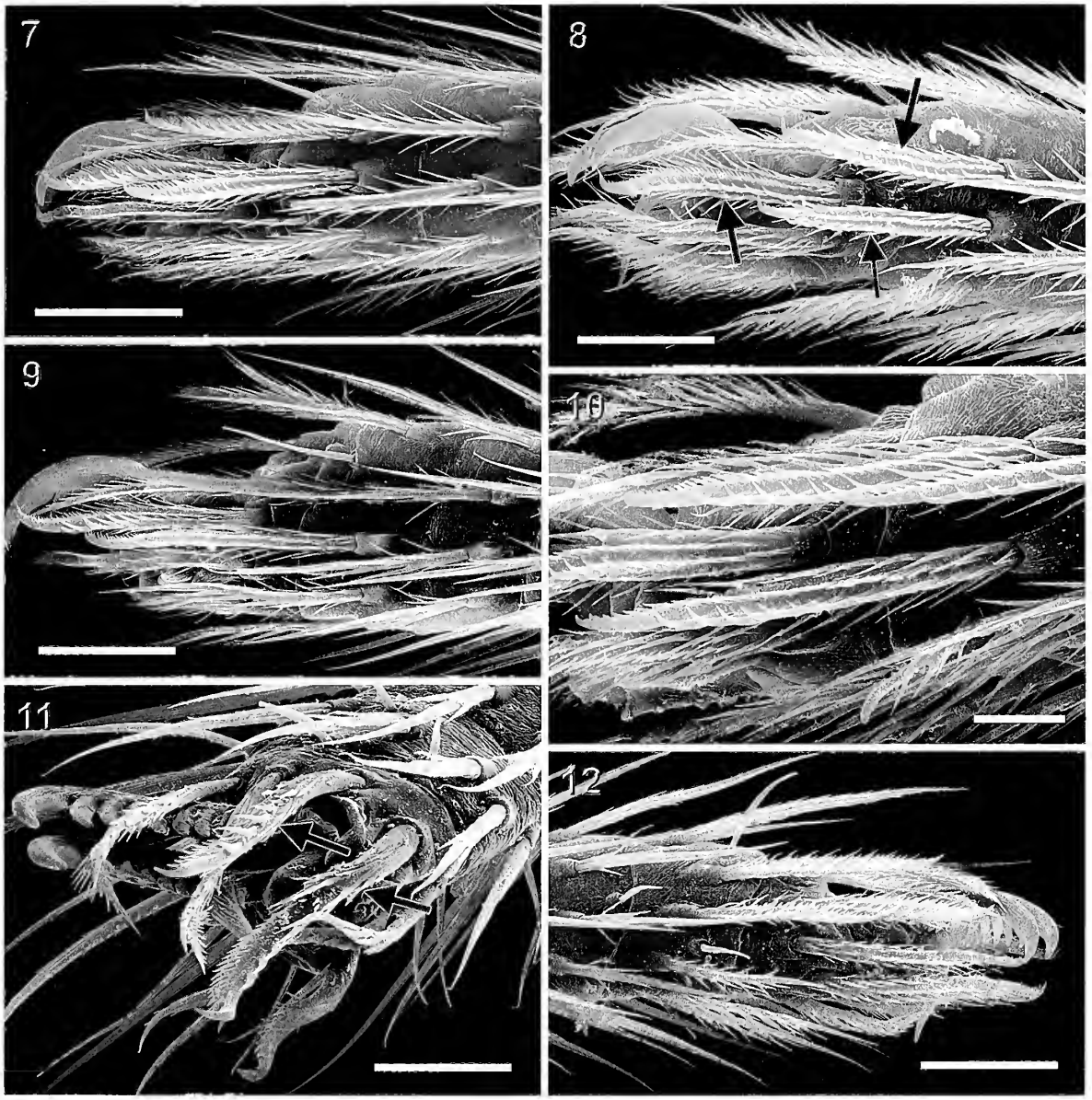
is at or near the base of Pholcidae, but the optimization is ambiguous. The cladogram suggests either one origin at the base of Pholcidae and subsequent loss in a subgroup of ninetines (this is the scenario shown in Fig. 32), or at least two independent gains.

With respect to comb-hair distribution on the tarsus, optimization suggests that a distal patch is plesiomorphic, ventral rows (double or single) are derived. The origin of ventral rows may have occurred more than once, at the base of Pholcinae and in certain "holocnemines." Another possible interpretation (which is shown in Fig. 32) is that comb-hairs arranged in rows are a synapomorphy of a subgroup of "holocnemines" + pholcines (see also Discussion below).

Comb-hair function.—Of the six specimens that were freeze-fixed during prey-wrapping, only one had a silk line in contact with a comb-hair. The silk line passed through the notch formed by one of the hooked branches (Fig. 31). In the other five specimens, no interaction between silk and comb-hairs could be observed; they had either been frozen at the wrong moment or the manipulations at preparing the object for the SEM had destroyed the functional contact between silk and comb-hairs.

DISCUSSION

Comb-hair evolution.—The data above suggest that pholcid comb-hairs evolved either once or twice. This uncertainty is related to the question of ninetine monophyly. If ninetines are in fact monophyletic (as in Fig. 32), then comb-hairs appear to have evolved either at least twice or once with at least one reversal. Paraphyletic ninetines, for example with Old World ninetines as sister to all other pholcids including New World ninetines, would suggest a single origin of pholcid comb-hairs without reversal. However, morphological data suggest that the Old World genus *Nita* is more closely related to some New World ninetines than to *Ninetis* (Huber & El Hennawy 2007). Ninetine monophyly is based mostly on morphological



Figures 7–12.—Hairs on tarsus 4 tip, New World clade. 7. *Modisimus guatuso*, female right tarsus 4, prolateral; 8. *Carapoia una* Huber 2005, female right tarsus 4, prolateral; 9. *Mesabolivar eberhardi*, male right tarsus 4, prolateral; 10. *Mesabolivar yuruani*, female right tarsus 4, prolateral-ventral; 11. *Priscula* sp., male right tarsus 4, prolateral-distal; 12. *Tainonia* sp., female left tarsus 4, prolateral. Arrows point to selected comb-hairs. Scale lines: 10 μm (10), 30 μm (8), 40 μm (7), 50 μm (9), 60 μm (11, 12).

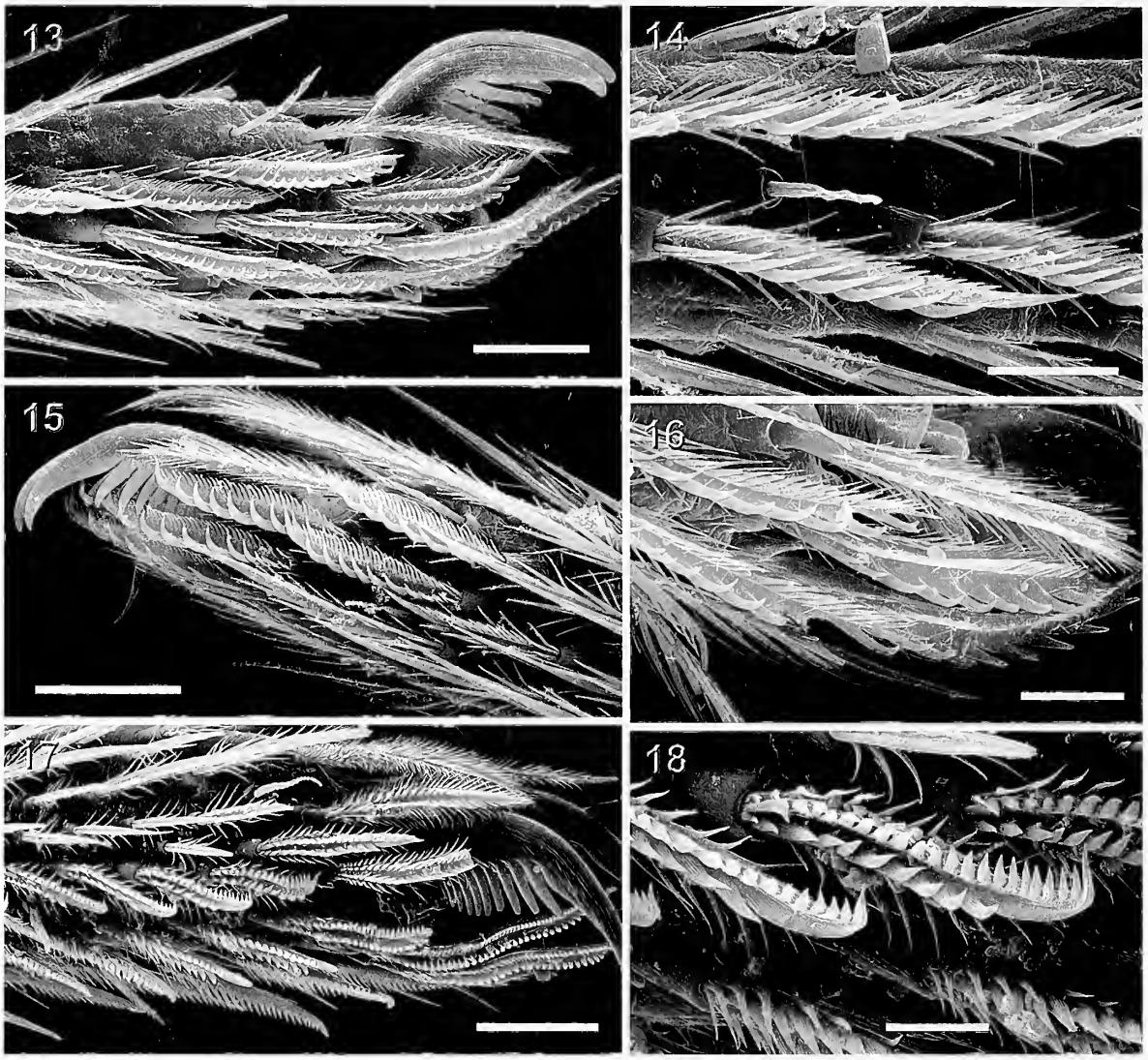
characters, some of which may not be independent due to their correlation with small size (Huber 2003d; Huber & Brescovit 2003). Molecular data appear promising for a solution of this question, but ninetines are notoriously rare in collections and only a few species have been included in recent molecular phylogenetic analyses (Bruvo-Madarić et al. 2005; Astrin et al. 2007).

Our data provide clear evidence for morphological simplification in pholeid comb-hair evolution. The simple *Pholcus*-type of comb-hair characterizes a highly derived clade within pholcines and the data unambiguously support its derivation from the complex *Belisana*-type. This clade of presently nine genera (all included in Table 1) is currently under revision by the first author, and preliminary cladistic analysis suggests that it is supported by at least one further morphological character, a bulbal apophysis traditionally called an appendix.

The lower number on branches in adult than in juvenile *P. phalangioides* comb-hairs could be interpreted as ontogenetie evidence for the evolutionary simplification of comb-hair morphology.

Comb-hair distribution provides further (though weak) evidence against holocnemine monophyly. One subgroup of holocnemines (*Holocnemus*, *Crossopriza*, *Smeringopus*, *Hoplopholcus*, *Smeringopina*) shares with pholcines the derived condition of comb-hairs not restricted to distal patches but being spread over most of the tarsus length. Holocnemine monophyly has been questioned before, first because morphological data appeared unconvincing (Huber 2000), later because molecular data suggested polyphyly (Bruvo-Madarić et al. 2005; Astrin et al. 2007).

The fact that pholcid comb-hairs originated distally on the tarsus suggests that they may be derived from those hairs that

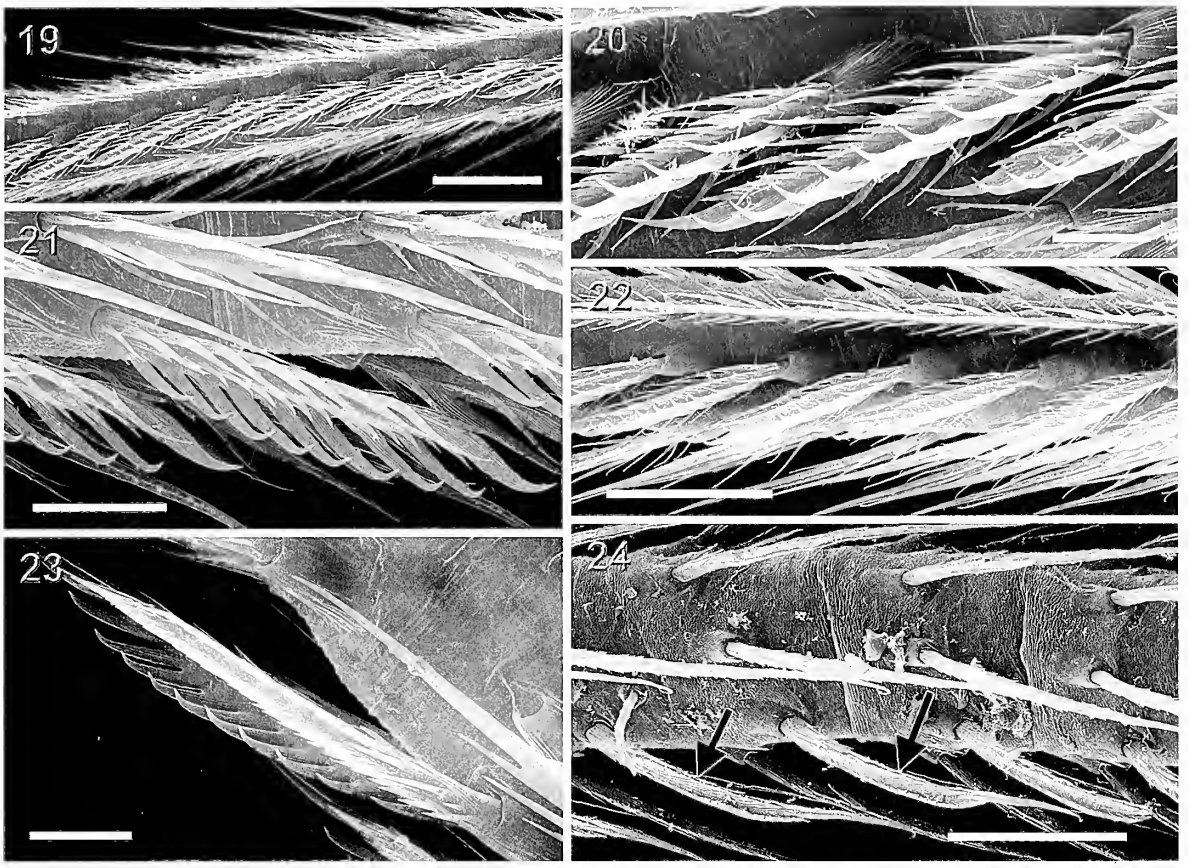


Figures 13–18.—Hairs on tarsus 4, "holocnemines." 13. *Hoplopholcus minotaurus*, female left tarsus 4, prolateral; 14. *Smeringopina pulchra*, female tarsus 4, ventral; note two rows of comb-hairs; 15. *Physocyclus globosus*, female right tarsus 4, prolateral; 16. *Trichocyclus nullarbor*, female left tarsus 4, prolateral; 17, 18. *Artema atlanta*, female left tarsus 4, prolateral. Scale lines: 20 μm (14, 16, 18), 40 μm (13), 50 μm (15), 70 μm (17).

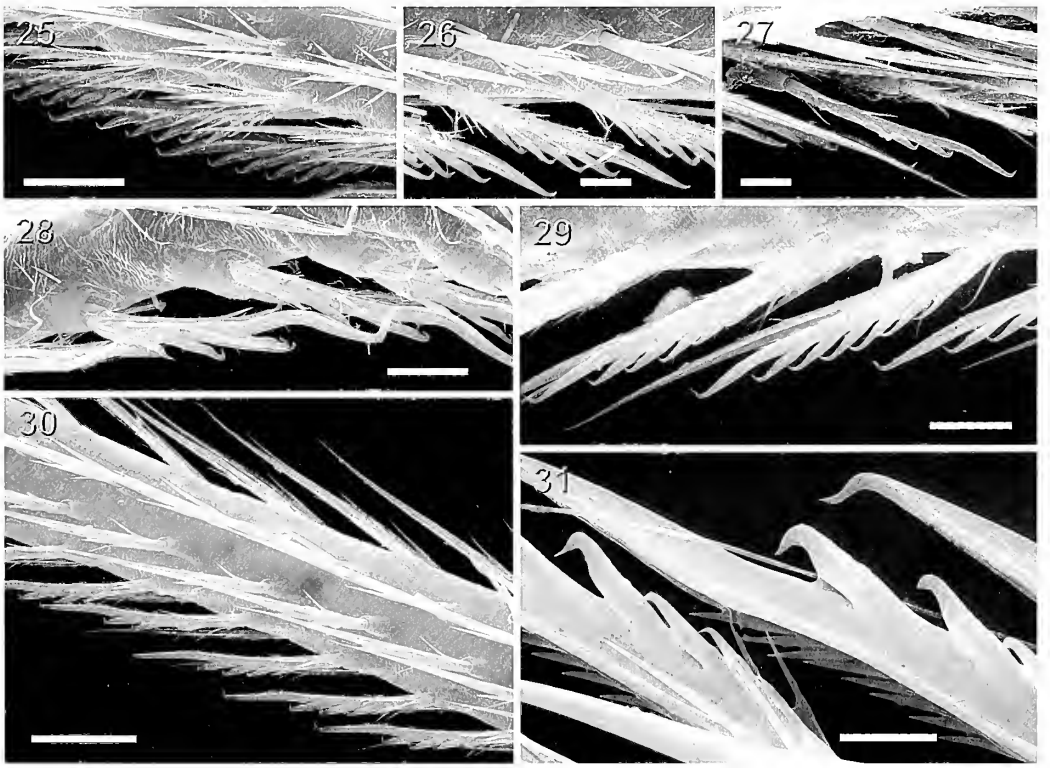
grasp silk in functional correlation with the median claw in many spider families (the "accessory claws" of Nielsen 1932; see figures 14–16 in Foelix 1970). This scenario is speculative, but recruitment of structures functioning in a closely related context appears more parsimonious than *de novo* modification of mechanoreceptors unrelated to silk manipulation. The similarity between comb-hairs and accessory claws has also been noted in theridiids (Agnarsson 2004: 591).

Comb-hair function.—Previous data (Kirchner & Opderbeck 1990) as well as our data on details of comb-hair function are very preliminary. Obviously, our method of spraying spiders during wrap attack, the transfer into ethanol, and the subsequent manipulations preparing the object for the SEM minimize the chances for the silk lines to remain in functional contact with the comb-hairs. However, we see no reason to assume that the hair running through the notch in Fig. 31 is just an artifact. We hypothesize that this is at least close to the actual method of contact, but we are aware that most questions in this regard remain unanswered: Why does a sticky silk line not adhere permanently to a comb-hair? How does a comb-hair "grasp" a line to pull it out of the spigot? What exactly happens when a silk line is released by the comb-hair? What is the function of the additional rows of branches in the *Belisana*-type of hair? The size of the structures involved, as well as the high amplitude and speed of the wrapping movements (usually < 0.5 s per cycle in *P. phalangioides*; Jackson & Brassington 1987; Kirchner & Opderbeck 1990) makes this appear a rather daunting challenge for future research.

Given this relative lack of detailed knowledge on comb-hair function, alternative functional interpretations must be considered. Pholcids and theridioids share a further, unusual character, i.e., the use of gumfoot lines (for pholcids see Japyassú & Macagnan 2004). However, not all pholcids studied use gumfoot lines while all pholcids studied use ss-wrap. In addition, pholcids apply the sticky droplets to the gumfoot line when returning to the sheet (Japyassú & Macagnan 2004), which means that the fourth legs do not



Figures 19–24.—Hairs on tarsus 4, "basal" Pholcines. 19, 20. *Paramicromerys scharffi*, female right tarsus 4, prolateral-ventral; 21. *Belisana ketambe* Huber 2005, female left tarsus 4, prolateral; 22. *Buitinga asax*, male right tarsus 4, prolateral; 23. *Spermophora senoculata*, female right tarsus 4, prolateral; 24. *Spermophora kerinci* Huber 2005, female left tarsus 4, prolateral. Arrows point to selected comb-hairs. Scale lines: 10 μm (20, 21, 23), 30 μm (24), 40 μm (19, 22).



Figures 25–31.—Hairs on tarsus 4, *Pholcus* and close relatives. 25. *Micropholcus fauroti*, male right tarsus 4, prolateral; 26. *Utlina luzonica*, female left tarsus 4, prolateral; 27. *Calapnita phyllicola*, male left tarsus 4, prolateral; 28. *Micromerys daviesae*, male left tarsus 4, prolateral; 29. *Pehrforsskalia conopyga*, male right tarsus 4, prolateral; 30. *Panjange uirabilis*, female right tarsus 4, prolateral; 31. *Pholcus phalangioides*, female tarsus 4 hairs with silk line freeze-fixed during wrap-attack. Scale lines: 10 μm (26-29, 31), 20 μm (25), 30 μm (30).

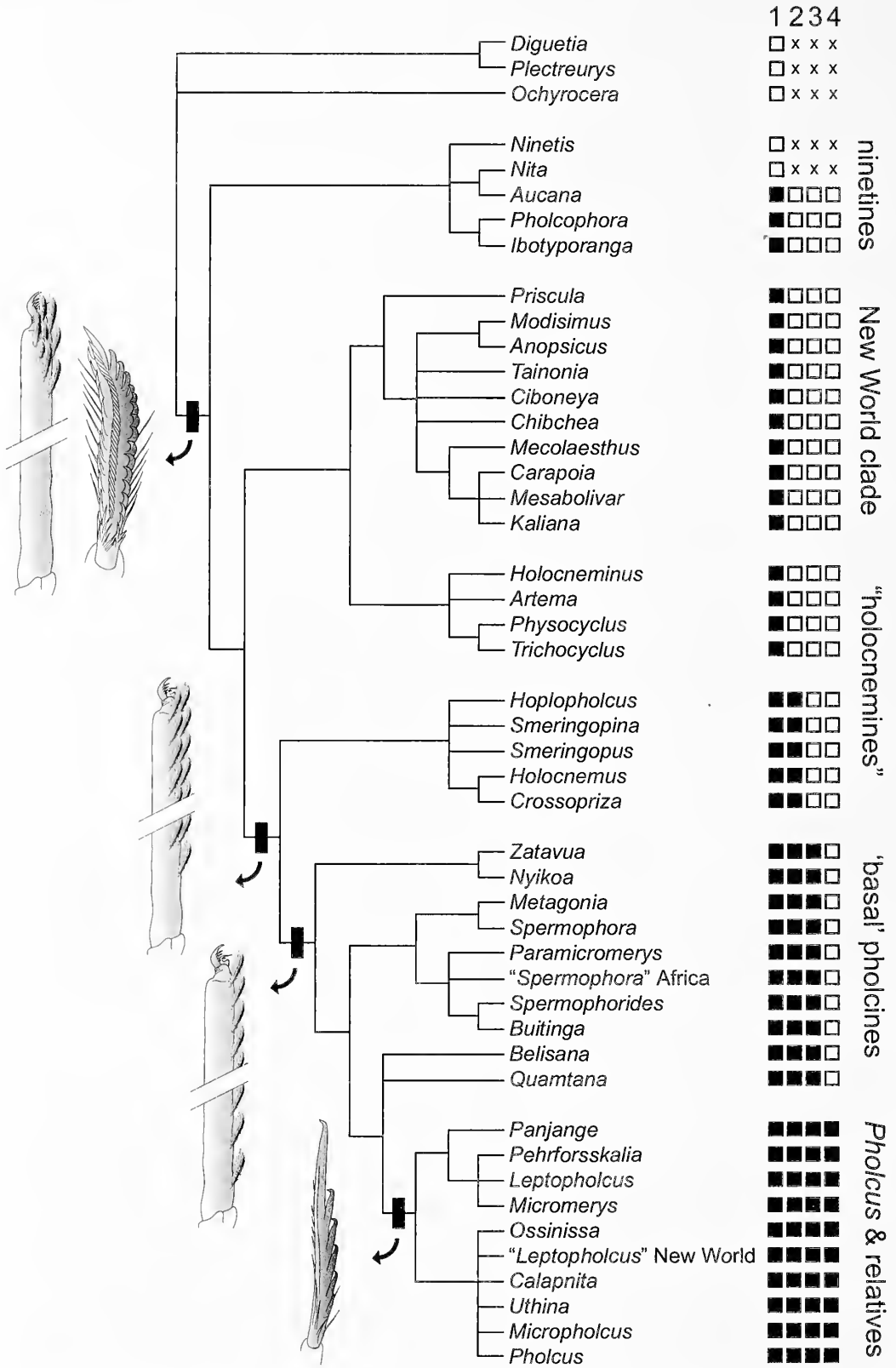


Figure 32.—Cladogram of Pholcidae derived from various previous works using molecular and morphological characters (Huber 2000, 2001, 2003a, b, c, 2005a, b; Bruvo-Madarić et al. 2005; Huber & El Hennawy 2007; Astrin et al. 2007; B.A. Huber unpublished data on *Pholcus* and close relatives). Only taxa studied herein are included (except for *Khorata* whose position within pholcines remains obscure). Hashmarks and figures at the left indicate hypothesized evolutionary changes: Origin of comb hairs (complex, in distal patches; see text for apparent seeondary reduction in Old World ninetines); Elongation of patch to cover most or entire tarsus length; Reduction to a single ventral row; Simplification of comb-hair. Character states for each taxon are shown at the right: (1) Comb-hair absent vs. present; (2) Distal patch vs. long row(s); (3) Patch or two rows vs. single row; (4) Complex vs. simple comb-hair.

manipulate sticky silk during gumfoot production (in contrast to ss-wrap). We interpret this as evidence for the hypothesis that comb-hairs function in the context of ss-wrap rather than gumfoot production.

We would like to point out that a similar unsolved problem exists in the analogous case of cribellate silk that is pulled out by a comb of hairs on the fourth metatarsus in cribellate spiders. These hairs are usually strongly sculptured, and in some species they carry multiple combs with over 3000 teeth per hair (Foelix & Jung 1978 on *Hypochilus thorelli* Marx 1888). How exactly the silk is grasped and released by the hairs seems to remain unknown.

Comparison with theridiids.—Theridiid comb-hairs have been known for a long time, and numerous illustrations of a variety of taxa exist in the literature (e.g., Kropf 1990; Agnarsson 2004; Knoflach & Pfaller 2004). However, we know of no systematic effort to summarize and characterize the morphological variation within the family. The only exception (Kasal 1997) appears rather incomprehensive, lacking detail, and based on purely speculative evolutionary reasoning. Published SEM photographs show that there is considerable variation of comb-hairs among theridiid taxa (but the view is often not given), and that in some taxa the hairs are quite similar to those of certain pholcids. Theridiid comb-hairs seem to be consistently spread over the entire length of the tarsus. Like in pholcids, no data on the functional details are available.

Comb-hairs in other taxa.—Comb-hairs have been reported in a number of other taxa, but the functional context is different from that in pholcids and theridioids in most or all of them. The homology of synotaxid comb-hairs with those of theridioids remains unclear. Agnarsson (2003) writes that the "serrated setae on the fourth tarsus of *Synotaxus* ...share little similarity with the theridiid comb," and concludes that these are "superficial similarities." In a cladistic analysis of theridiids and relatives by the same author (Agnarsson 2004), the data suggest that comb-hairs are a synapomorphy of the "spineless femur clade," a group including theridioids plus synotaxids and cyatholipids. The observation by Coddington (1986: 335) of ss-wrap in *Synotaxus* strengthens the idea that synotaxid comb-hairs, even though morphologically different and not present in all species (Exline & Levi 1965) are homologous to those of theridioids.

In the anapid *Comaroma simoni* Bertkau 1889, comb-hairs have been found on all tarsi. They appear to function in the context of cleaning (Kropf 1990). Very distinctive comb-hairs have been found on the third legs of certain *Mesabolivar* (Pholcidae) species (E. Machado, pers. comm.). Their function remains unknown, but there might be some correlation with the sexually dimorphic modification of male third legs (thickened femora) in certain *Mesabolivar* species. Thickened male third femora also occur in some other pholcid genera (Huber 1994, 2000: p. 17) but the third tarsal hairs of these taxa remain unstudied.

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Himalmartensus, a new genus of the spider family Amaurobiidae from Nepal (Araneae)

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Abstract. A new genus of Amaurobiidae, *Himalmartensus*, is described from Nepal, and includes three species: the type species *H. martensi* new species, *H. ausobskyi* new species, and *H. nepalensis* new species. Members of this new genus can be separated from other amaurobiid genera by the combination of the following characters: the presence of a colulus, a single chilum, smooth trichobothrial bases, and simple tracheal tubes. Both promargin and retromargin of *Himalmartensus* chelicerae have 5–8 teeth and the female epigynum is modified with long and looping copulatory ducts. The spinnerets of all three new species are described and tracheal tubes of *H. martensi* are examined. Spinnerets, colulus, chilum and tracheal tubes of *Himalmartensus* are compared to similar genera, including amaurobiids, agelenids, and cybaeids. *Himalmartensus* is defined as a member of the family Amaurobiidae because of its similarity to the amaurobiids *Rubrius* and *Macrobunus*.

Keywords: Taxonomy, new species, Himalayas

The definition of the family Amaurobiidae Thorell 1870 is fraught with problems (Griswold 1990). Lehtinen (1967) attempted to define the Amaurobiidae, Agelenidae, and other families of his superfamily Amaurobioidea but his treatment suffered from a vagueness of character definition (Griswold 1990). Griswold also indicates that the problem of defining Amaurobiidae becomes one of discovering synapomorphies and any taxon assigned to the Amaurobiidae should be demonstrably related to the type genus of the family, *Amaurobius* C.L. Koch 1837. Griswold (1990), the author who most recently tried to define Amaurobiidae, defines the family as having a divided cribellum, the simple, sclerotized retrolateral and dorsal tibial processes on the male palp, and two rows of metatarsal and a single row of tarsal trichobothria (sensu Lehtinen 1967). Since then, the subfamily Phyxelidinae Lehtinen 1967 from Africa has been elevated to family Phyxelididae and placed as sister group of Titanoecidae by Griswold et al. (1999). The currently included members of the family Amaurobiidae are still globally distributed (Platnick 2008), including at least the Holarctic genera of the subfamily Coelotinae F.O. Pickard-Cambridge 1893, the Holarctic *Amaurobius* C.L. Koch 1837 and related genera, the Holarctic genus *Arctobius* Lehtinen 1967, the Neotropical *Macrobunus* Tullgren 1901, *Rubrius* Simon 1887 and related genera, and a few other genera from Africa. The relationship of Amaurobiidae to other families has for a long time been, and remains, one of the major cladistic problems in spider taxonomy (Coddington & Levi 1991). The intrafamilial relationships and monophyly of Amaurobiidae have only recently begun to be addressed using morphological (Griswold et al. 2005) and molecular data (Wu et al. 2002; Bi et al. 2005; Spagna & Gillespie 2008). However, these works use only a limited number of representative amaurobiid taxa and, clearly, further phylogenetic work is urgently needed.

Griswold (1990) addressed the higher level taxonomic question of the familial relationships of Phyxelidinae by emphasizing four character systems: the nature of the cribellum; the presence, form, number, and position of processes on the male palpal tibia; the pattern of tarsal and metatarsal trichobothria; and the form of the tracheal system. In examining those structures, we found that the striated texture of the small trichobothrial hood, plus the presence of PMS paracribellar spigots and PLS modified spigot (amaurobiid PLS spigot of Wang 2000), are unique and define *Amaurobius* (the type genus of the family) and related genera including, at least, *Callobius* Chamberlin 1947, *Pimus* Chamberlin 1947 and *Taira* Lehtinen 1967. This "true Amaurobiidae" group has been tested phylogenetically by Griswold et al. (2005). As a result, the family Amaurobiidae includes at least the above genera, and more are likely to be included with more detailed analysis that is beyond the scope of this study.

Wu et. al (2002) analyzed 12S rRNA gene sequences using 2 amaurobiid species, *Coelotes plancyi* Simon 1880 and *Tangrinia tibetana* (Hu & Li 1987) and 2 agelenid species of the genus *Agelena* and concluded that *Coelotes* is more closely related to *Tangrinia* than to *Agelena*. However, in another study (Bi et al. 2005) that used 18S and 28S rRNA in an attempt to resolve the phylogenetic position of Coelotinae, four taxa from two amaurobiid and two agelenid genera (e.g., *Draconarius*, *Coelotes*, *Agelena*, and *Alloagelena*) were used and results indicated that *Coelotes* + *Draconarius* are more closely related to *Agelena* + *Alloagelena* than to *Tangrinia*, suggesting (*Tangrinia*((*Coelotes*, *Draconarius*)(*Agelena*, *Alloagelena*))), which is in conflict with the findings of Wu et al. (2002). More recently, the analyses by Spagna & Gillespie (2008) using molecular data of non-orb-weaving spiders suggested a sister group relationship between Coelotinae and Ageleninae, which is consistent with the conclusion of Bi et al. (2005). Spagna & Gillespie (2008) found that Agelenidae (including Ageleninae and Coelotinae) could be the sister to Hahniidae + Cybaeidae related taxa. In addition to agelenids and coelotines, Spagna & Gillespie also selected four taxa for analyses from three "true amaurobiids" genera (e.g., *Amaurobius*, *Callobius*, and *Pimus*) and found none of them was closely related to Coelotinae. Unfortunately, other lineages of current Amaurobiidae species were not sampled by Spagna & Gillespie (2008) (e.g., *Rubrius* and *Macrobunus* related species from South America, the Holarctic *Arctobius*, and *Tangrinia* from the Himalayan region) and their phylogenetic placements, either related to Agelenidae or to Amaurobiidae, still need further investigation. The synapomorphies of current Agelenidae (including Coelotinae) are still unknown, but some

may be found in their spinneret structures. Both Ageleninae and Coelotinae are ecribellate spiders and build similar funnel-shaped webs (and also the cribellate amaurobiid genus *Tamgrinia*) (Wang 2002, 2003), although the webs of Coelotinae appear to be much smaller. It seems likely that species of the cribellate *Tamgrinia* are also related to agelenids and coelotines.

When we first examined the three amaurobiid species collected from Nepal and included in this paper, their generic placement was puzzling. After eight years of a failed search for male specimens in hopes of obtaining additional characters to support their generic status, we decided to publish the material on hand as a new genus, *Himalmartensus*, based only on females. Hopefully males will be found in the future based on our published female information. Even without male palpal characters, the differences between *Himalmartensus* new genus and other current amaurobiid and agelenid members are obvious. We defined this new genus as a member of the family Amaurobiidae because of its similarity to amaurobiid *Rubrius* and *Macrobunus*, despite the large geographic distance between them. Of course, the phylogenetic placement of *Rubrius* and *Macrobunus* related amaurobiids needs to be evaluated further. Of the similar genera (Table 1), the new genus *Himalmartensus* is similar to *Rubrius* and some *Macrobunus* species by having a single hairy colulus (Figs. 9, 27, 29), rather than a cribellum found in "true amaurobiids," *Tamgrinia*, *Arctobius*, and some *Macrobunus*, or two patches of setae as in the subfamily Coelotinae, Ageleninae, and the family Cybaeidae. Another similarity between *Himalmartensus* new genus and *Rubrius* is the smooth large hood of the trichobothrial base (Figs. 12, 26, 51), being either longitudinally or transversely striated in other studied taxa. But the four simple tracheal tubes in *Himalmartensus* new genus (Fig. 36) differ from the strongly branched tracheal tubes in *Rubrius*. While in *Cybaeus jilinensis* (Song et al. 1993), there are only two tracheal tubes, which are strongly branched (Fig. 61). In addition, the female epigynum of *Himalmartensus* new genus is modified with long and looping copulatory ducts. Similar coiled copulatory ducts are observed in coelotine *lutulentus*-group species and also in some Cybaeidae species, for example, *Cybaeina minuta* (Banks 1906), but the species of *Himalmartensus* new genus show no evidence of complex spermathecal pore structures as in Cybaeidae. According to Bennett (1992), the complex spermathecal pore structures are also absent in Coelotinae and other amaurobiids.

METHODS

All measurements are in millimeters. Unless indicated otherwise, all scale bars are 0.2 mm length. Legs are not measured. Spinnerets, trichobothria, and tarsal organs are examined using SEM. Other photos are taken from the Olympus Stereo Scope eyepiece using a Nikon Coolpix 4500 camera. Prior to SEM examination, the specimens were either air-dried or critical point dried and coated. Tracheal tubes were examined using Griswold's (1990) method. The spigot names used in the text and figures follow Coddington (1989) and Griswold (1990). The distribution map was generated using GIS ArcView software and the .dbf files of the studied species are downloadable from http://www.amaurobiidae.com, which is published and maintained by Xin-Ping Wang. More photos of the type specimens included in this paper can be viewed from the website http://www.ChineseSpecies.com which was created and maintained by Shu-Qiang Li and Xin-Ping Wang.

The types are deposited in the Senckenberg Museum, Frankfurt, Germany (SMF). Abbreviations: AC = aciniform spigots; ALE = anterior lateral eyes; ALS = anterior lateral spinneret; AME = anterior median eyes; CY = cylindrical spigots; mAP = minor ampullate spigots; MAP = major ampullate spigots; PI = piriform spigots; PLE = posterior lateral eyes; PLS = posterior lateral spinneret; PME = posterior median eyes; PMS = posterior median spinneret.

SYSTEMATICS

Family Amaurobiidae Thorell 1870

Himalmartensus Wang & Zhu new genus

Type species.—*Himalmartensus martensi* Wang & Zhu new species.

Other species.—*Himalmartensus ausobskyi* Wang & Zhu new species and *H. nepalensis* Wang & Zhu new species.

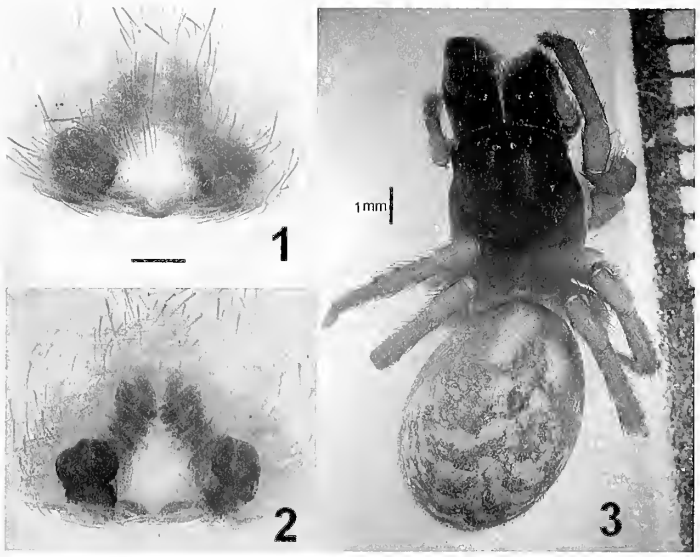
Etymology.—The genus is named in honor of Jochen Martens (Mainz, Germany) for his contribution of amaurobiid specimens that were collected from his Himalayan expeditions. These specimens included a new coelotine genus (*Himalcoelotes* Wang 2002) and 10 species of this genus (Wang 2002). Another 38 coelotines, including 36 new species, have been recognized from Martens material and will be published soon. The gender is masculine.

Diagnosis.—*Himalmartensus* new genus can be diagnosed from other amaurobiids, agelenids, and genera of other related families by at least: (1) AMS represented by colulus as in *Rubrius* and some *Macrobunus* species; (2) single chilum, as in *Rubrius*, and *Amaurobius*-related genera; (3) smooth trichobothrial base, as in *Rubrius* and agelenids, all others being either longitudinally or transversely striated, and (4) four simple tracheal tubes, but branched tubes in *Cybaeus*, *Rubrius* and *Macrobunus*. In addition, both the promargin and retromargin of *Himalmartensus* new genus have 5–8 teeth and the epigynum is modified with long and looping copulatory ducts.

Description.—Females: Medium size ecribellate spiders, with total length 8–10 mm. Carapace elongate, reddish brown, slightly narrowed in ocular area, sparsely covered with short, long black setae; few strong setae on clypeus, ocular area, and middle carapace; longitudinal fovea moderately depressed. Legs moderately long. Abdomen dark brown, with dark maculation, heavily covered with short setae (Figs. 3, 14, 15, 23, 33, 37, 45). Spinnerets short. From dorsal view, anterior eye row slightly procurved, posterior row procurved; eye sizes and arrangements: AME smallest, ALE and PLE largest and subequal, PME larger than AME, AME–AME separated by approximately AME diameter, AME–ALE widely separated by approximately 1–1.5 AME diameter, ALE–PLE separated by approximately their radius, PME–PLE and PME–PME distinctly separated by approximately 1.5–2 times PME diameter, AME–PME widely separated by at least 2 times AME diameter (Figs. 6, 16, 42). Clypeus height 1.5–2 times AME diameter, covered with long, strong setae; chilum undivided, hairless (Figs. 6, 16). Chelicerae with 6–7 promarginal teeth, the basal ones largest, and 5–8 retromarginal teeth,

Table 1.—Comparison of eight selected characters of twelve representative species from ten Amaurobiidae genera: *Amaurobius, Callobius, Taira, Tamgrinia, Arctobius, Pinus, Macrobunus, Rubrius, Himalmartensus,* and *Coelotes*, Agelenidae genus *Agelena*, and Cybaeidae genus *Cybaeus.*

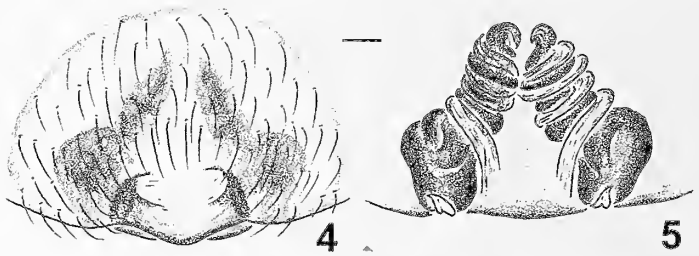
Characters	*Amaurobius fenestralis*	*Callobius bennetti*	*Taira sp.*	*Tamgrinia laticeps*	*Arctobius ageleneides*	*Pinus pitus*	*Macrobunus multidentatus*	*Rubrius antarcticus*	*Himalmartensus martensi* (Figs. 14–36)	*Coelotes atropos* (Wang 2002)	*Cybaeus spp.* (Figs. 60, 61)	*Agelena labyrinthica* (Fig. 58)
AMS	cribellum	cribellum	cribellum	cribellum	cribellum	cribellum (Griswold et al. 2005)	colulus (Griswold et al. 2005)	colulus	colulus	setae	setae (Bennett 1988)	setae (Roth & Brame 1972)
Cribellum	divided	divided	divided	divided	divided	–	–	–	–	–	–	–
PMS paracribellar spigots	present	present	present	absent	absent	present	absent	absent	absent	absent	absent	absent
PLS modified spigot (amaurobiid PLS spigot of *Wang 2000*)	present	present	present	absent	absent	present	absent	absent	absent	absent	absent	absent
Chilum	single	single	single	paired	paired	?	absent	single	single	paired	paired (Ihara & Nojima 2004)	paired
Trichobothria base, large hood striations	transverse	transverse	transverse	transverse	transverse	transverse	longitudinal	smooth or finely striated	smooth	transverse	smooth or finely striated longi-tudinally	smooth
Trichobothria base, small hood striations	striated	striated	striated	smooth	smooth	striated	smooth	smooth	smooth	smooth	smooth	smooth
Tracheal middle tubes	four simple tubes	four simple tubes (Griswold et al. 2005)	four simple tubes	four simple tubes	?	four simple tubes (Griswold et al. 2005: *Pinus* sp.)	four tubes, with median tubes slightly branched (Griswold et al. 2005)	four tubes, with median tubes strongly branched	four simple tubes	four simple tubes	two strongly branched tubes	four simple tubes



Figures 1–3.—*Himalmartensus ausobskyi* new species, female holotype (# 44) from Jiri valley, Dholakha District, Nepal, photos. 1. Epigynum, ventral view; 2. Epigynum, dorsal view; 3. Habitus, dorsal view.

with basal large and distal small; condyle large; dorsal chelicerae covered with long setae, with strongly elevated base; chelicerae ventrally flat, with proximal short setae and inner long, fine setae; fangs moderately long; anterior face of chelicerae covered with dense, long, strong setae (Figs. 22, 44). Endites elongated, with anterior scopula and linear serrula. Labium longer than wide, slightly notched distally. Sternum shield-shaped, sparsely covered with long dark setae, heavily sclerotized (Figs. 7, 17, 43). Legs medium length, I, IV longest, almost subequal, leg III shortest; trochanters not notched; tibiae with about four rows of trichobothria; metatarsi and tarsi with one row of trichobothria; trichobothria with both large and small hoods smooth, not striated (Figs. 12, 26, 51). Tarsal organ with simple opening (Figs. 13, 28, 52). Tarsi with three claws, superior claws with 8–10 teeth; scopulae absent; leg spination often varies among individuals, typical leg spination pattern: femur: I p0–0–2, d1–1–0; II p0–0–1, d1–1–0; III p0–0–1, d1–1–0; IV d1–1–0; tibia: I p0–0–1, v2–2–2; II p0–0–1, v2–2–2; III p0–0–1, v1–2–2; IV d1–0–0; r1–1–0, v1–1–2; metatarsus: I v2–2–2; II v2–2–2; III p0–1–1, r0–1–1, v2–2–2; IV d0–0–1, v1–1–2. Tracheal tubes simple, limited to abdomen; spiracle situated close to spinnerets and connected to relatively narrow atrium from which two lateral and two median tubes arise (Fig. 36). Colulus present, covered with hairs (Figs. 9, 27); ALS short, apex with 2 major ampullate gland spigots (MAP) and 41–55 piriform gland spigots (PI); PMS small, with 2 minor ampullate gland spigots (mAP), 2 aciniform gland spigots (AC), and 1–3 cylindrical gland spigots (CY); PLS second segment short, with approximately 6–17 aciniform gland spigots, and 2 cylindrical gland spigots (Figs. 8–11, 29–32, 47–50). Epigynum simple, atrium small, situated close to epigastric furrow; copulatory ducts long, with 3–7 loops around spermathecae; spermathecae with bases relatively large, widely separated, anteriorly converging with spermathecal heads almost touching each other (Figs. 1, 2, 4, 5, 18–21, 24, 34, 35, 38–41, 46).

Males: unknown.



Figures 4, 5.—*Himalmartensus ausobskyi* new species, female holotype (# 44) from Jiri valley, Dholakha District, Nepal, drawings. 4. Epigynum, ventral view; 5. Epigynum, dorsal view.

Distribution.—Nepal (Fig. 53).

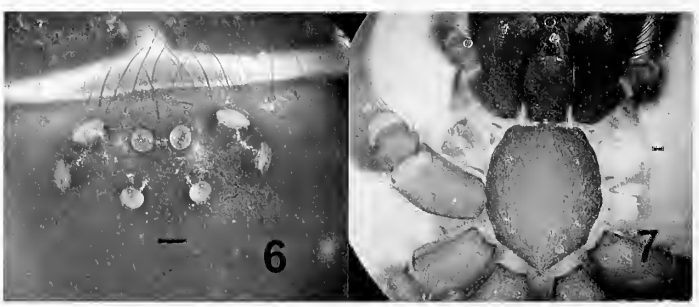
***Himalmartensus* ausobskyi** Wang & Zhu new species
Figs. 1–13, 53

Type specimens.—NEPAL: holotype female, *Dholakha District*, Jiri valley, elev. 2600–3000 m, oak forest, 86°14′E, 27°37′N, 16 January 1970, J. Martens (SMF, #44); 1 female paratype, *Lalitpur District*, Phulchoki Mt., foot-hills near Godavari, elev. 1770 m, 85°23′E, 27°36′N, 19 March 1980. J. Martens & A. Ausobsky (SMF, #105).

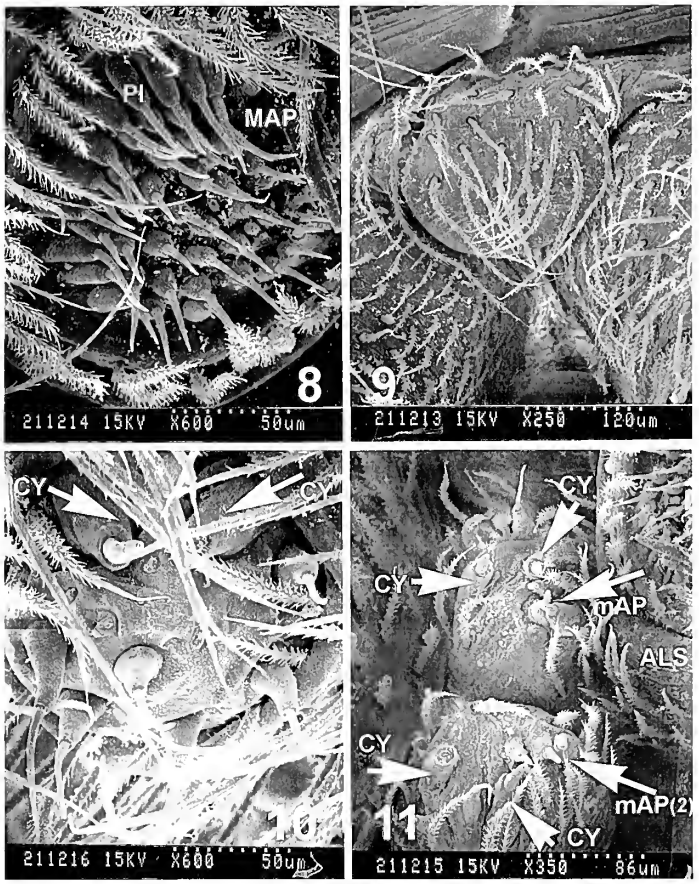
Etymology.—The specific name is after Albert Ausobsky, one of the collectors of the type specimens.

Diagnosis.—*H. ausobskyi* resembles *H. nepalensis* in having long spermathecal stalks (short in *H. martensi*), with long copulatory ducts that loop around spermathecal stalks at least four times, and the narrow, less sclerotized posterior plate of atrium. The spermathecal stalks of this species converge gradually while extending anteriorly (Figs. 2, 5), rather than converging immediately as in *H. nepalensis*.

Description.—Holotype female: Total length 11.3. Carapace 4.80 long, 3.60 wide. Abdomen 6.50 long, 4.90 wide (Fig. 3). Eye sizes and interdistances: AME and PME approximately same size, ALE largest, PLE slightly smaller than ALE (AME 0.16, ALE 0.26, PME 0.17, PLE 0.20); AME separated from each other by 2/3 of its diameter, from ALE by slightly more than AME diameter, from PME by approximately 1.5 times AME diameter; PME and PLE widely separated (AME–AME 0.10, AME–ALE 0.21, AME–PME 0.25, PME–PME 0.31, PME–PLE 0.34) (Fig. 6). Chelicerae with 6 promarginal, and 8 retromarginal teeth. Apex of ALS with 2 major ampullate gland spigots (MAP) and approximately 44 piriform gland spigots (PI); PMS with 2 minor ampullate gland spigots (mAP), 2 aciniform gland spigots (AC), 2 cylindrical gland

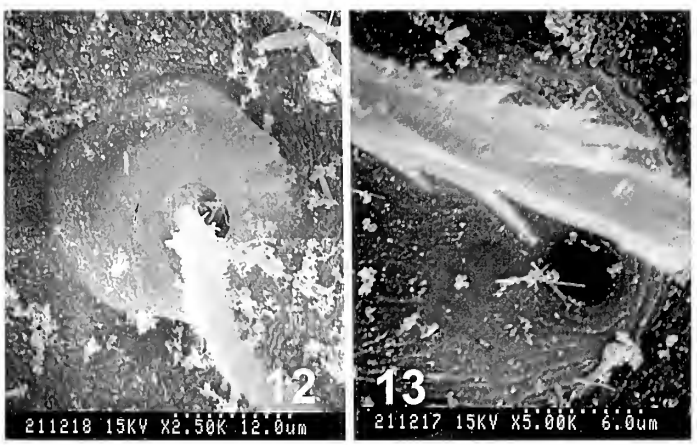


Figures 6, 7.—*Himalmartensus ausobskyi* new species, female holotype (# 44) from Jiri valley, Dholakha District, Nepal, photos. 6. Eyes and chilum, dorsal view; 7. Sternum area, ventral view.

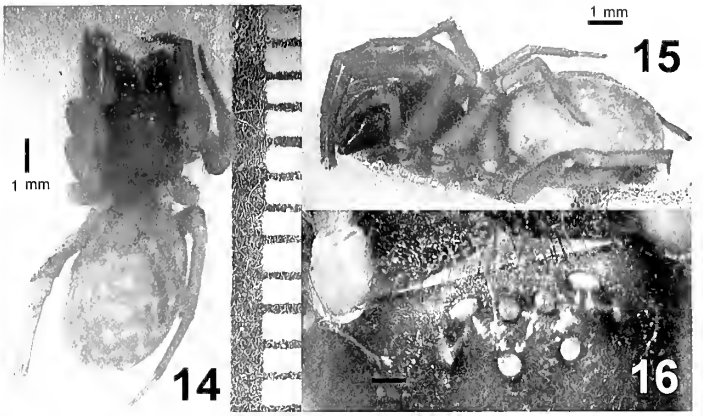


Figures 8–11.—*Himalmartensus ausobskyi* new species, female holotype (# 44) from Jiri valley, Dholakha District, Nepal, SEM, spinnerets in ventral view. 8. ALS (left); 9. Colulus; 10. PLS (left); 11. PMS.

spigots (CY); PLS with approximately 6 aciniform gland spigots, and 2 cylindrical gland spigots (Figs. 8–11). Epigynum with small atrium; atrium with narrow, less sclerotized posterior plate; copulatory ducts originate posteriorly between the spermathecal bases, extending anteriorly, each looping around the long and converging spermathecal stalks at least four times; spermathecae with large bases separated by



Figures 12, 13.—*Himalmartensus ausobskyi* new species, female holotype (# 44) from Jiri valley, Dholakha District, Nepal, SEM. 12. Trichobothrium; 13. Tarsal organ.



Figures 14–16.—*Himalmartensus martensi* new species, female holotype (# 36) from Kathmandu District, Kathmandu valley, Balaju Park, Nepal, photos. 14. Habitus, dorsal view; 15. Habitus, lateral view; 16. Eyes and chilum, dorsal view.

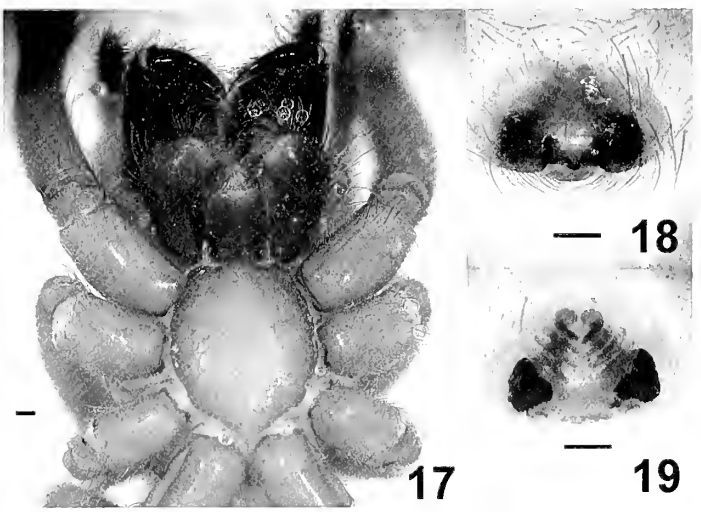
approximately their width; spermathecal stalks extend anteriorly, converging gradually, with distal ends close together (Figs 1, 2, 4, 5).

Males unknown.

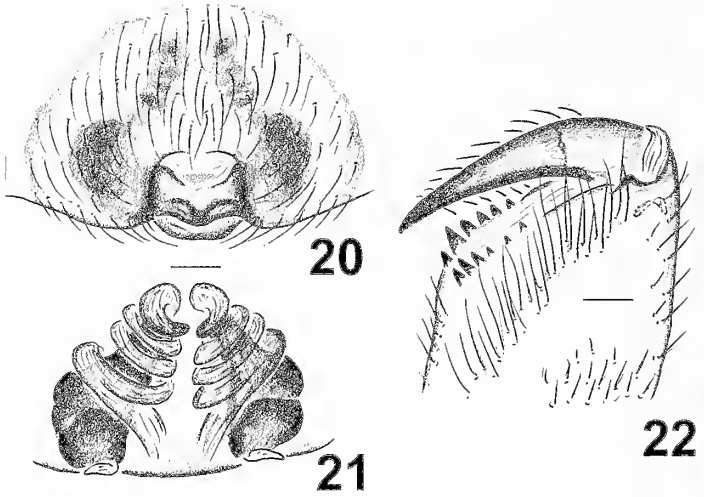
Distribution.—Nepal (Dholakha, Lalitpur) (Fig. 53).

Himalmartensus martensi Wang & Zhu new species
Figs. 14–36, 53

Type specimens.—NEPAL: holotype female, *Kathmandu District*, Kathmandu valley, Balaju Park, elev. 1400 m, 85°17′E, 27°44′N, 1 May 1973, J. Martens (SMF, #36); 1 female paratype, *Lamjung District*, Marsyandi valley, between Tal and Dharapani, forest remnants in gorge, elev. 1580–1850 m, 84°21′E, 28°17′N, 12 April 1980. J. Martens & A. Ausobsky (SMF, #136); 1 female paratype, *Ilam District*, Mai Pokhari, elev. 2100–2200 m, Castganopsis forest remnants, 87°55′E, 26°58′N, 9–10 April 1988, J. Martens & W. Schawaller (SMF, #319, tracheal tubes examined); 1 female paratype, *Myagdi District*, southern Dhaulagiri range, Bobang



Figures 17–19.—*Himalmartensus martensi* new species, female holotype (# 36) from Kathmandu District, Kathmandu valley, Balaju Park, Nepal, photos. 17. Sternum area, ventral view; 18. Epigynum, ventral view; 19. Epigynum, dorsal view.



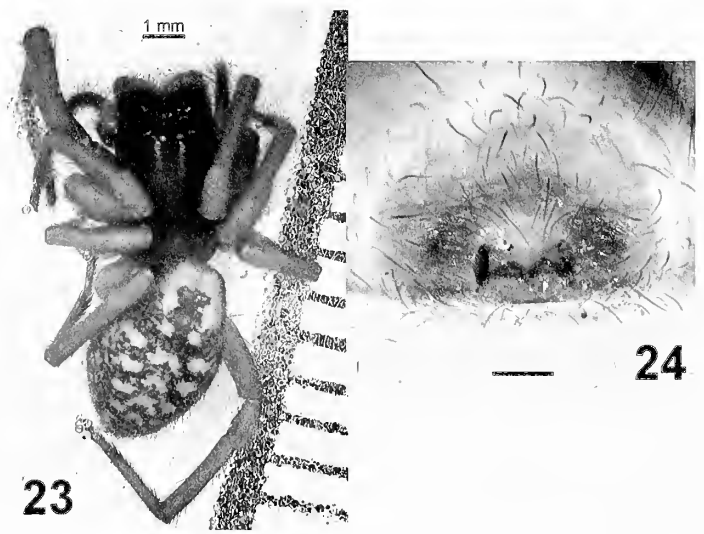
Figures 20–22.—*Himalmartensus martensi* new species, female holotype (# 36) from Kathmandu District, Kathmandu valley, Balaju Park, Nepal, drawings. 20. Epigynum, ventral view; 21. Epigynum, dorsal view; 22. Chelicera, ventral view.

S of Dhorpatan, elev. 2500 m, 26 April–1 May 1970, J. Martens (SMF, #3); 1 female paratype, *Makawanpur District*, Mahabarat Mts., Daman, elev. 2500–2900 m, 22–25 February 1970, J. Martgens (SMF, #33).

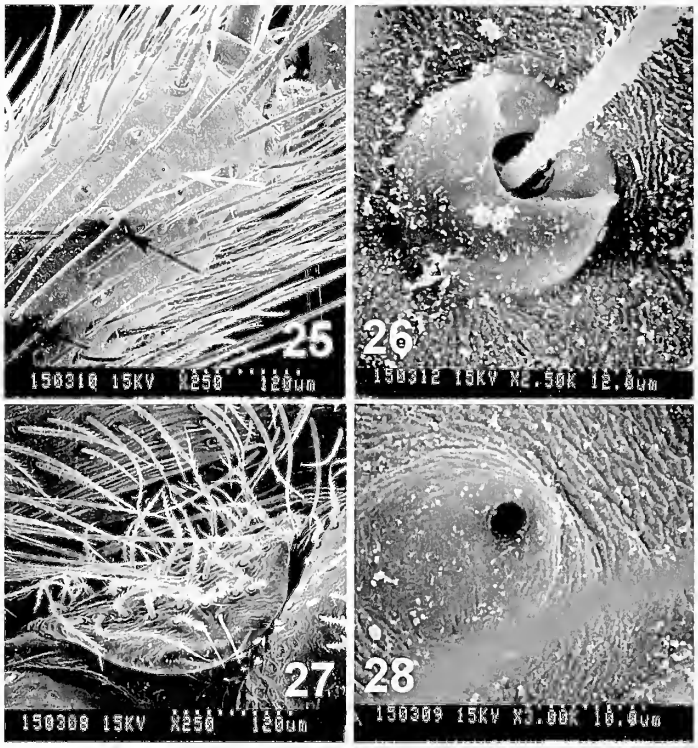
Etymology.—This new species is named in honor of Jochen Martens who collected the specimens used in this and other studies.

Diagnosis.—Compared to the more than four copulatory duct loops in *H. ausobskyi* and *H. nepalensis*, this new species has only 3 loops around the relatively short spermathecal stalk (Figs. 19, 21, 35). In addition, the atrium of this new species has a broad, highly sclerotized plate (Figs. 18, 20, 24, 34).

Description.—Holotype female: Total length 11.3. Carapace 3.10 long, 2.30 wide. Abdomen 5.20 long, 3.40 wide (Figs. 14, 15). Eye sizes and interdistances: AME and PME subequal, ALE largest, PLE slightly smaller than ALE (AME 0.13, PME 0.14, ALE 0.18, PLE 0.16); AME separated from each other



Figures 23, 24.—*Himalmartensus martensi* new species, female paratype (# 319) from Ilan District, Mai Pokhari, Nepal, photos. 23. Habitus, dorsal view; 24. Epigynum, ventral view.



Figures 25–28.—*Himalmartensus martensi* new species, female paratype (# 3) from Bobang Sudl. Dhorpatan, Nepal, SEM. 25. Tarsus, showing position of tarsal organ (white arrow) and two distalmost trichobothria (black arrows); 26. Trichobothrium; 27. Colulus; 28. Tarsal organ.

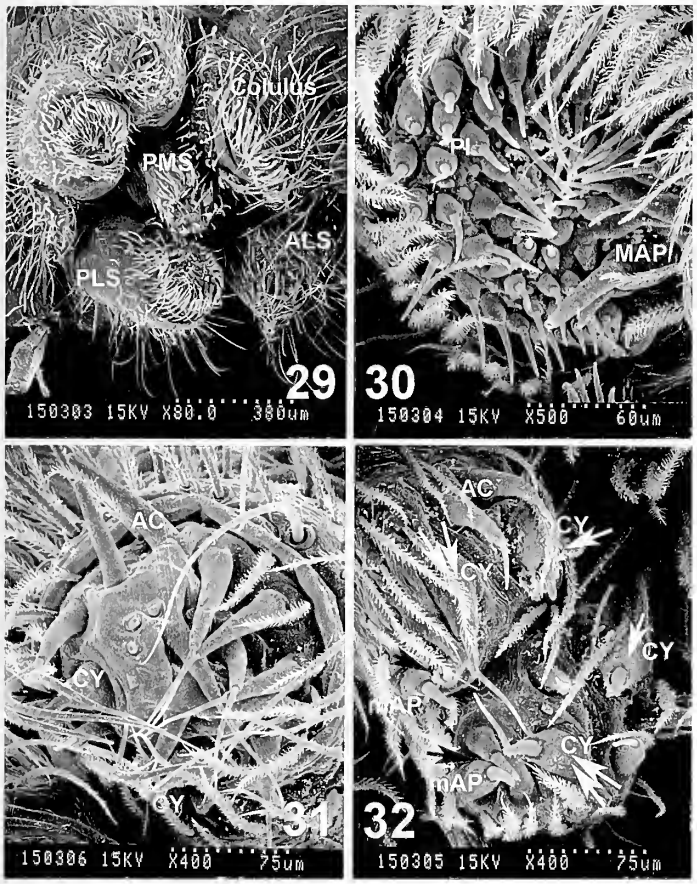
by 2/3 of its diameter, from ALE by about AME diameter, from PME by approximately 1.5 times AME diameter; posterior eyes widely separated (AME–AME 0.08, AME–ALE 0.13, AME–PME 0.19, PME–PME 0.23, PME–PLE 0.22) (Fig. 16). Chelicerae with 6 promarginal, and 6 retromarginal teeth (Fig. 22). Apex of ALS with 2 major ampullate gland spigots (MAP) and approximately 55 piriform gland spigots (PI); PMS with 2 minor ampullate gland spigots (mAP), 2 aciniform gland spigots (AC), and 2 cylindrical gland spigots (CY); PLS with approximately 10 aciniform gland spigots, and 2 cylindrical gland spigots (Figs. 29–32). Epigynum with small atrium; atrium with broad, highly sclerotized posterior plate; copulatory ducts originate posteriorly between the spermathecal bases, extend anteriorly and loop around the converging spermathecal stalks 3 times; spermathecae with large bases that are separated by approximately their width; spermathecal stalks extend anteriorly and converge gradually, with distal ends close together (Figs. 18–21).

Males unknown.

Distribution.—Nepal (Kathmandu, Lamjung, Ilan) (Fig. 53).

Himalmartensus nepalensis Wang & Zhu new species
Figs. 37–53

Type specimens.—NEPAL: holotype female, *Rasuwa District*, Trisuli Valley, Gosainkund, mixed forest, elev. 2400–2600 m, 85°23′E, 28°8′N, 23 April 1973 (SMF, #38); 1 female paratype, *Rasuwa District*, Trisuli Valley, Gosainkund, moist forest in gorge, elev. 1000–2000 m, 85°19′E, 28°8′N, 23 June?



Figures 29–32.—*Himalmartensus martensi* new species, female paratype (# 3) from southern Dhaulagiri range, Bobang S of Dhorpatan, Myagdi District, Nepal, SEM, spinnerets in ventral view. 29. Spinnerets, whole; 30. ALS (left); 31. PLS (right); 32.PMS.

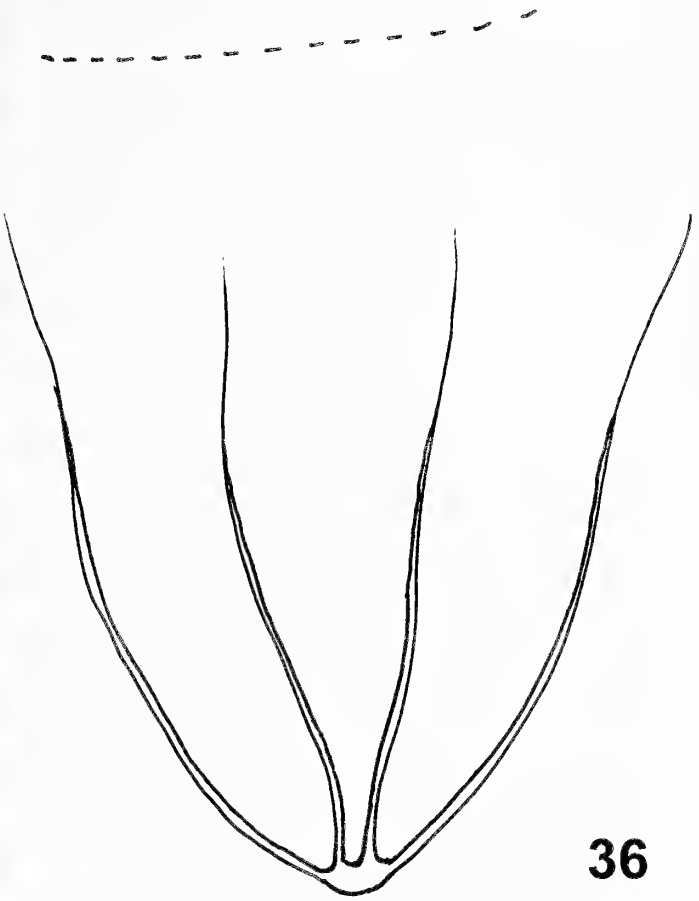
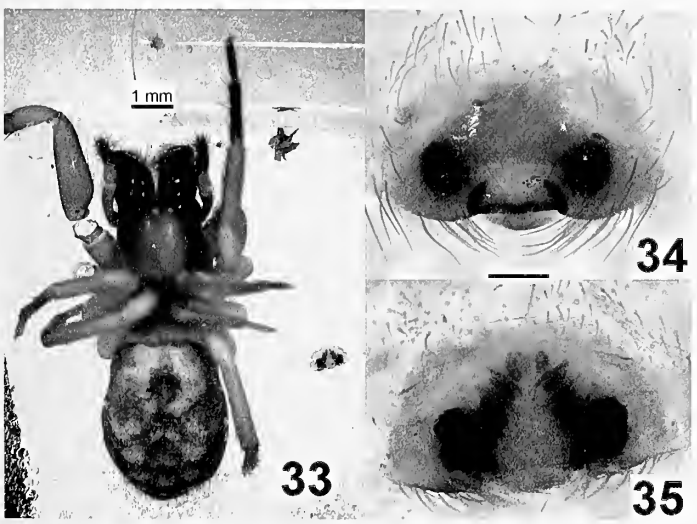
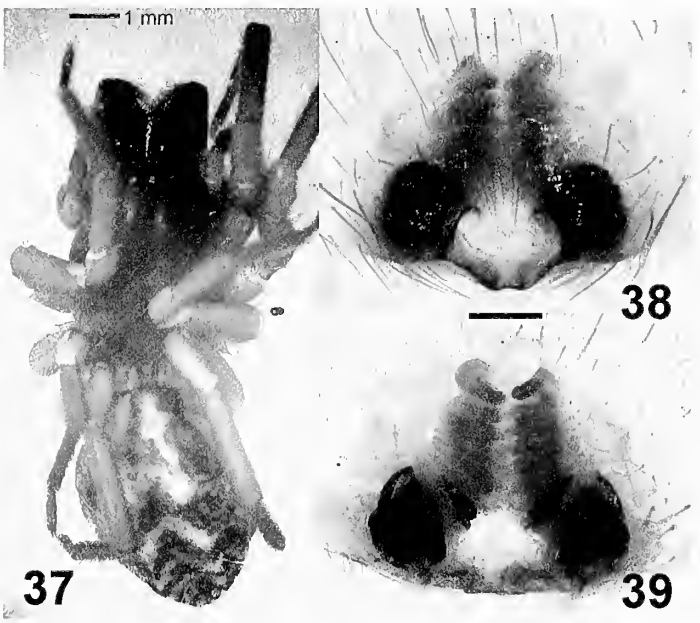


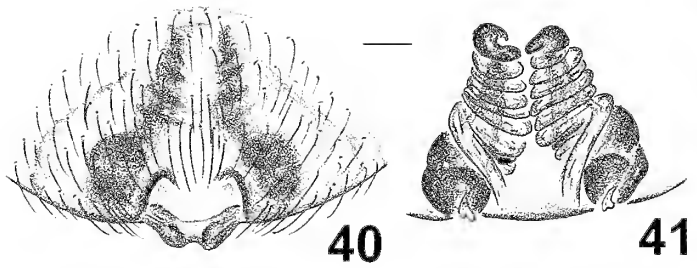
Figure 36.—*Himalmartensus martensi* new species, female paratype (# 319) from Ilan District, Mai Pokhari, Nepal, drawing, tracheal tubes.



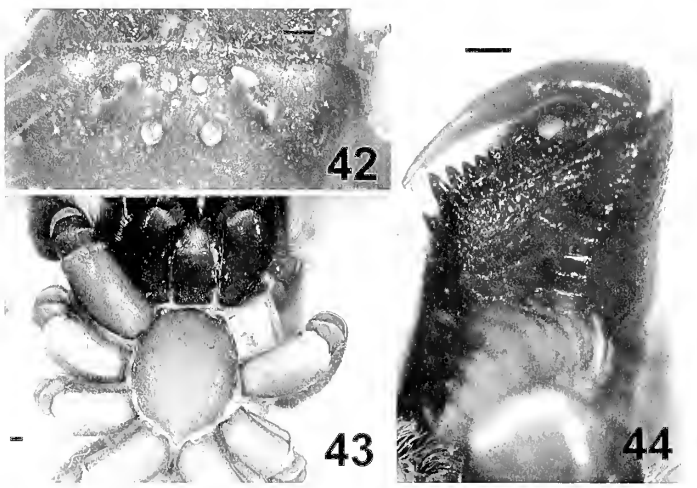
Figures 33–35.—*Himalmartensus martensi* new species, female paratype (# 33) from Mahabarat Mts., Daman, Makawanpur District, Nepal, photo. 33. Habitus, dorsal view; 34. Epigynum, ventral view; 35. Epigynum, dorsal view.



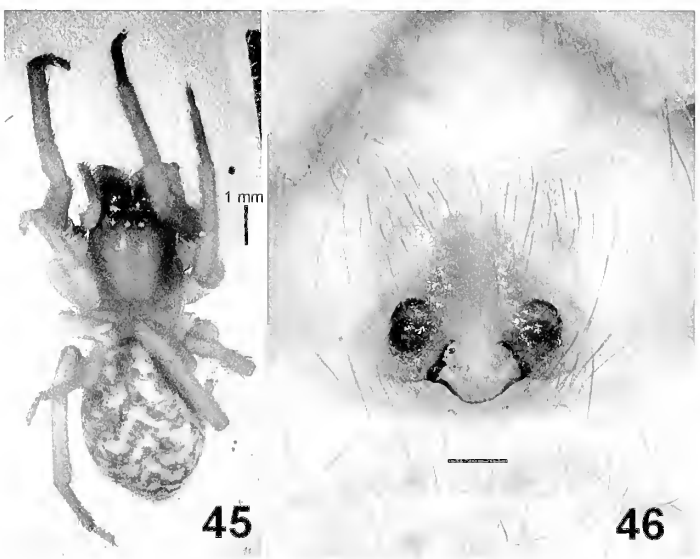
Figures 37–39.—*Himalmartensus nepalensis* new species, female holotype (# 38) from Trisuli valley, Gosainkund, Rasuwa District, Nepal, photos. 37. Habitus, dorsal view; 38. Epigynum, ventral view; 39. Epigynum, dorsal view.



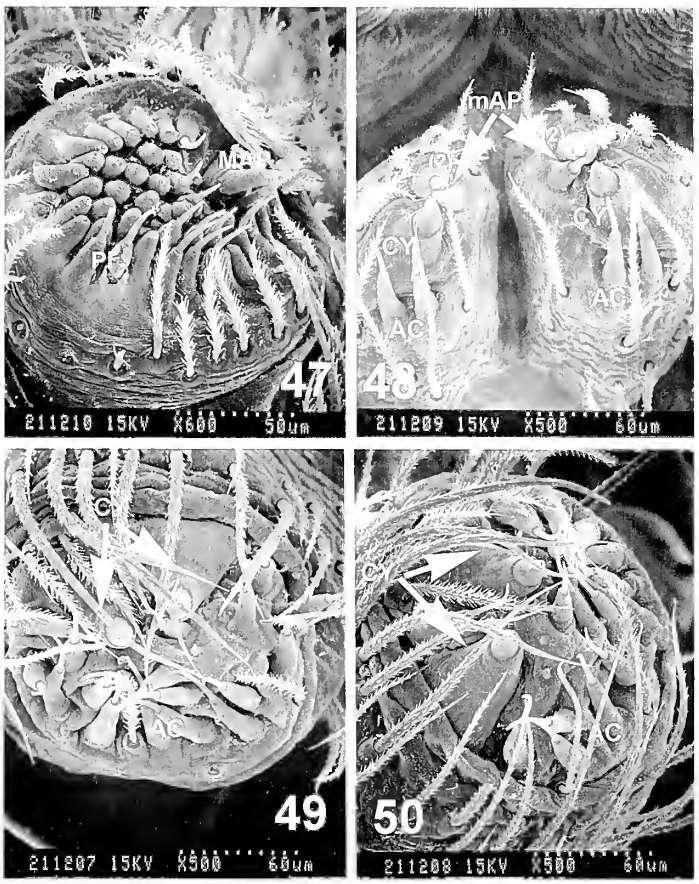
Figures 40, 41.—*Himalmartensus nepalensis* new species, female holotype (# 38) from Trisuli valley, Gosainkund, Rasuwa District, Nepal, drawings. 40. Epigynum, ventral view; 41. Epigynum, dorsal view.



Figures 42–44.—*Himalmartensus nepalensis* new species, female holotype (# 38) from Trisuli valley, Gosainkund, Rasuwa District, Nepal, photos. 42. Eyes, dorsal view; 43. Sternum area, ventral view; 44. Chelicera, ventral view.



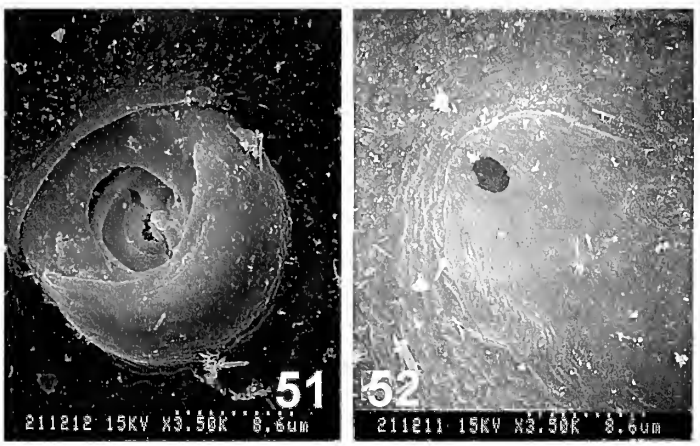
Figures 45, 46.—*Himalmartensus nepalensis* new species, female paratype (# 38A) from Trisuli valley, Gosainkund, moist forest in gorge, Rasuwa District, Nepal, photos. 45. Habitus, dorsal view; 46. Epigynum, ventral view.



Figures 47–50.—*Himalmartensus nepalensis* new species, female paratype (# 37) from Trisuli valley, between Ramche and Dhunche, Rasuwa District, Nepal, SEM, spinnerets in ventral view. 47. ALS (left); 48. PMS; 49. PLS(left); 50. PLS (right).

1973, J. Martens (SMF, #38A); 1 female paratype, *Rasuwa District*, Trisuli Valley, between Ramche and Dhunche, elev. 1800–2000 m, 85°14′E, 28°5′N, 22 April 1973, J. Martens (SMF, #37).

Etymology.—The specific name refers to the type locality of the species, Nepal.



Figures 51, 52.—*Himalmartensus nepalensis* new species, female paratype (# 37) from Trisuli valley, between Ramche and Dhunche, Rasuwa District, Nepal, SEM. 51. Trichobothrium; 52. Tarsal organ.

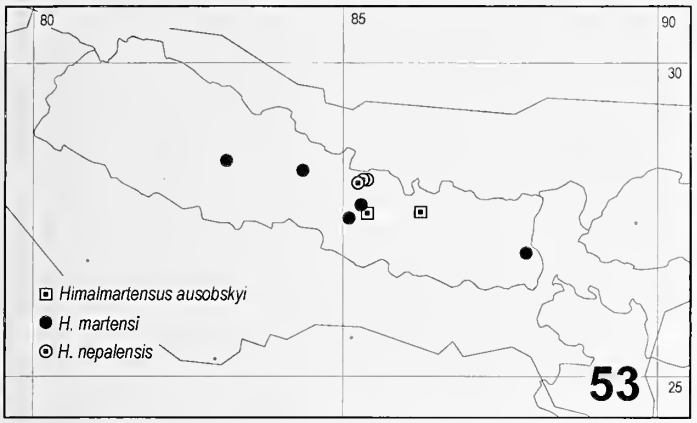
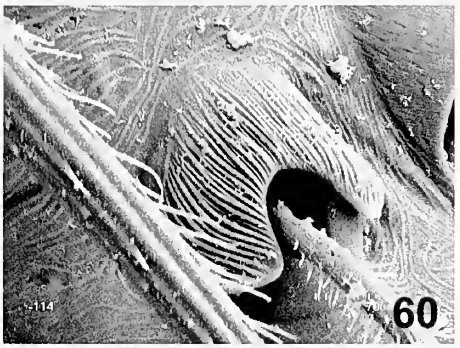


Figure 53.—Records of *Himalmartensus* new genus



Figures 60, 61.—Trichobothrium of *Cybaeus tetricus* (C.L. Koch 1839), with specimen from Europe; 61. Tracheal tubes of *Cybaeus jilinensis* (Song, Kim & Zhu 1993), with specimen from Jilin, China.

Diagnosis.—*H. nepalensis* is similar to *H. ausobskyi* in having long spermathecal stalks and copulatory ducts which loop at least 5 times, and the narrow, less sclerotized posterior plate of atrium. The spermathecal stalks of this new species converge immediately and then extend anteriorly (Figs. 39, 41), rather than converge gradually as in *H. ausobskyi*.

Description.—Holotype female: Total length 11.3. Carapace 4.20 long, 3.40 wide. Abdomen 4.60 long, 3.20 wide (Fig. 37). Eye sizes and interdistances: AME smallest, PME slightly larger than AME, ALE and PLE about the same size (AME 0.11, ALE 0.20, PME 0.15, PLE 0.18); AME separated from each other by less than its diameter, from ALE and PME by about 1.5 times AME diameter; posterior eyes are widely separated (AME–AME 0.08, AME–ALE 0.17, AME–PME 0.17, PME–PME 0.23, PME–PLE 0.26) (Fig. 42). Chelicerae with 7 promarginal and 5 retromarginal teeth (Fig. 44). ALS with 2 major ampullate gland spigots (MAP) and approximately 41 piriform gland spigots (PI); PMS with 2 minor ampullate gland spigots (mAP), 2 aciniform gland spigots (AC), and 1 cylindrical gland spigot (CY); PLS with approximately 17 aciniform gland spigots and 2 cylindrical gland spigots (Figs. 47–50). Epigynum with small atrium having a narrow, weakly sclerotized posterior plate; copulatory ducts originate posteriorly between the spermathecal bases, extend anteriorly and loop around the long and converging spermathecal stalks at least 6 times; spermathecae with large bases separated by approximately their width; spermathecal stalks extend anteriorly and converge gradually, with anterior ends contiguous (Figs. 38–41).

Males unknown.

Distribution.—Nepal (Rasuwa) (Fig. 53).

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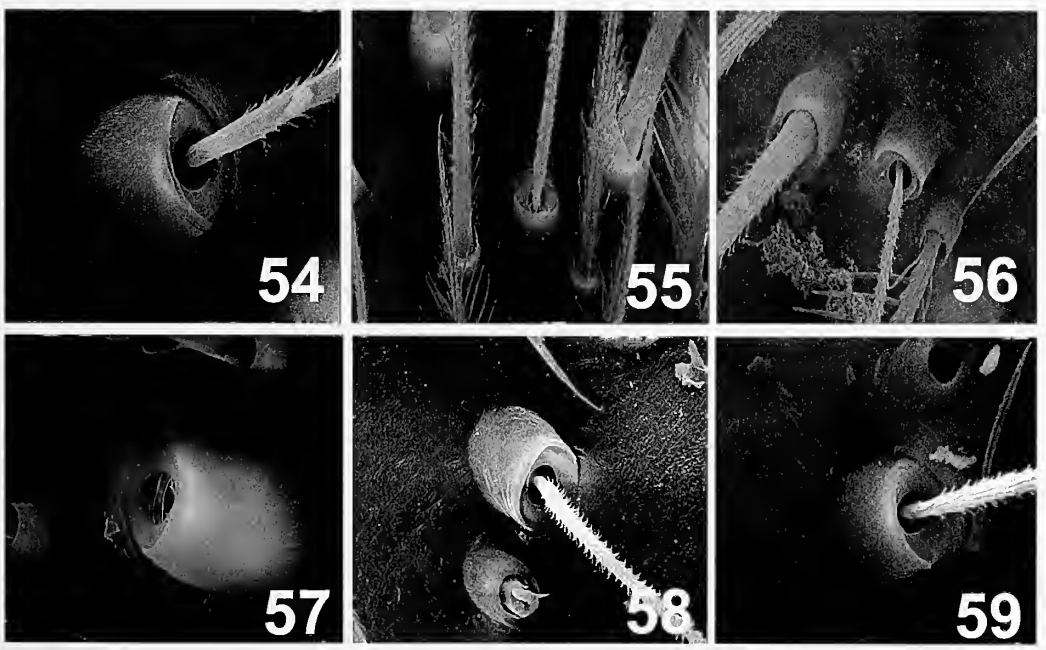

Figures 54–59.—Trichobothria of six agelenid species, with specimens collected from China (No detailed collection data linked to SEM photos). 54. *Agelena koreana* Paik 1965; 55. *Allagelena difficilis* (Fox 1936); 56. *Allagelena bistriata* (Grube 1861); 57. *Agelena silvatica* Oliger 1893; 58. *Agelena labyrinthica* (Clerck 1757); 59. *Huangyuania tibetata* (Hu & Li 1987).

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Diversity and composition of spider assemblages in five vegetation types of the Terai Conservation Area, India

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Abstract. This study deals with the comparison of spider diversity and composition in a complex landscape of the Terai Conservation Area (TCA) characterized by alluvial floodplains of tall grassland interspersed with woodland, swamps, and riparian patches. High water table, annual flooding, and annual grassland fire maintain its dynamic complexity. A mosaic of five vegetation types was sampled for spiders from March 2005 to August 2006 by using pitfall traps and other semi-quantitative collection methods along transects. A total of 3666 adult spiders representing 22 families, 60 genera, and 160 species were found. Using the abundance-based estimator, Chao1, the predicted richness for the total area sampled is 173 ± 8.32 (SD) species. This indicates that the inventory was almost complete at the regional scale (92%). With similar proportions of captured species, rarefied richness value showed that species richness was highest in riparian swamp forest. Comparison of different sites revealed that species composition was much more similar within the same vegetation type than among different vegetation types. Assemblage composition differed the most between riparian swamp forest and plantation. Guild structure varied considerably in relation to the structural quality of vegetation.

Keywords: Terai ecosystem, species richness, species composition, guild structure

A central theme in community ecology is the understanding of what drives the variation in species diversity and composition (MacArthur 1972; Holyoak et al. 2005); the interest is not in knowing the exact number and identity of every species at a given site, but rather how the diversity and composition vary among sites. High diversity and complex interactions pose challenges to studies of ecological processes (Halaj et al. 2000). One approach to investigate multispecies systems is to focus on dominant taxa or a key assemblage, which is potentially critical for local community food-web dynamics (Polis & Strong 1996). Spiders are an excellent example of such a group because they are widespread intermediate-level predators and are among the most diverse groups on earth (Coddington & Levi 1991; Wise 1993). Moreover, spiders appear to be good subjects for studying biodiversity patterns (Platnick 1999) as their distribution and occurrence are strongly influenced by habitat structure and vegetation parameters (Greenstone 1984; Uetz 1991; Wise 1993; Buddle et al. 2000; de Souza & Martins 2004). The present study was carried out in the Terai Conservation Area (TCA), which represents the Terai landscape, one of the most diverse ecosystems of India (Kumar et al. 2002). This landscape is characterized by a complex of sal forest, tall grassland, and swamps maintained by periodic flooding. The knowledge of diversity and distribution of spiders in this area is sparse as compared to other Indian regions. In the present study we documented the richness and composition of ground and above ground spiders across five different vegetation types of TCA. Using this information, the community structure of spider assemblages in different vegetation types was compared, and the possible effect of habitat characteristics on species occurrence and observed pattern was explained.

METHODS

Study Area.—The study was conducted in the alluvial flood plains of TCA that cover an area of 7,896.6 km^2 between the Himalayan foothills and the Gangetic plains in the state of Uttar Pradesh, India (27°49′–28°43′N, 81°01′–81°18′E) from March 2005 to August 2006. TCA is made up of a spatially heterogeneous landscape of forest-grassland-wetland complex within a matrix of extensive agricultural land and with sparsely distributed habitations (Kumar et al. 2002). The terrain is on the flat flood plains of the Suheli, Mohana, and Sharda rivers. The climate of TCA is tropical monsoon type. The TCA experiences three distinct seasons: winter (November–March), summer (April–June), and monsoon (July–October).

We sampled spiders in localities across five vegetation types that contained contiguous and relatively homogeneous areas of each vegetation community. The vegetation types are as follows:

(a) Riparian Swamp Forest: This forest type was found in swampy depressions along streams and remains under water continuously for a long period during the rains or where deep black heavy waterlogged soils occur and is structurally characterized by extremely diverse overstorey and understorey structure relative to other vegetation types. This densely vegetated forest type is associated with rich humus soil. The most common tree species were *Syzygium cumini*, *Barringtonia acutangula* (patches occurred along rivers), *Trewia nudiflora*, *Terminalia alata*, *Lagerstromea parviflora*, and *Ficus racemosa*. *Clerodendrum viscosum*, *Glycosmis pentaphylla*, and *Murraya koenigii* are the prominent shrubs. *Ageratum conyzoides*, *Dioscorea belophylla*, and *Corchorus aestuans* were the important herbs in this type of forest. *Syzygium cumini* formed a dense crop with long clean boles. Structurally, these forests typically have a mixture of sparse and closed canopy, a diverse understorey, and a deep layer of leaf litter.

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(b) Grassland: Grasslands occurred in low-lying areas or depressions, which were waterlogged or marshy in nature. Such areas had alluvial soils, mostly sandy with clayey patches. These depressions mark old river channels. Structurally, these grasslands are characterized by an absence of trees and moderate to low herbaceous ground cover. Floristically, these grasslands were composed primarily of native and introduced grass species and a few scattered shrubs. These areas are annually burnt as part of the management practices in TCA. Prominent tree species were *Bombax ceiba*, *Ficus racemosa*, and *Syzygium cumini*. Prominent grasses were *Arundo donax*, *Phragmites karka*, *Themeda arundinacea*, *Sclerostachya fusca*, *Saccharum spontaneum*, and *Saccharum narenga*. The grasslands have interspersed swamps.

(c) Pure Sal Woodland: This vegetation type represents moist deciduous forest that occurs on higher alluvial terraces. *Shorea robusta* (Sal) occupied a major part of this woodland. This woodland was often associated with flat topography and loamy soil. Variation in overstorey structure is limited by the dominance of *Shorea* and the understorey structure is relatively diverse, composed of *Ardisia solanacea*, *Colebrookia oppositifolia*, *Clerodendrum viscosum*, and *Murraya koenigii*. Woody climber *Tiliacora acuminata* formed a dense carpet on the ground in several patches.

(d) Mixed Sal Woodland: This was the rarest vegetation type, which occurred only in five patches in the entire study area and was confined to the gentle slopes and old river terraces around grasslands. The overstorey was composed of old *Shorea robusta* with *Bridelia squamosai*, *Bauhinia racemosa*, *Mallotus philippensis*, *Syzygium cumini*, and *Terminalia alata*. Mixed Sal woodlands are structurally characterized by closed overstorey of *Shorea robusta* and *Terminalia alata*, while the dense understorey layer is composed of *Ardisia solanacea*, *Clerodendrum viscosum*, and *Glycosmis pentaphylla*.

(e) Plantation: Extensive plantations of *Acacia catechu*, *Ailanthus excelsa*, *Bombax ceiba*, *Dalbergia sissoo*, *Eucalyptus citriodora*, and *Tectona grandis* have been raised as gap planting as well as after clear felling. This vegetation type mostly represents large scale mechanized plantations of teak (*Tectona grandis*) and *Eucalyptus*. It was chosen to represent disturbed conditions since most of the patches were close to villages and on the periphery of the protected areas and continue to undergo grazing and other biomass extraction to varying extents. Structurally, plantations are characterized by moderate to low canopy cover and least herbaceous ground cover.

Sampling methods.—Spiders were collected along 50 m × 10 m transects, with 20 transects per vegetation type. These transects were treated as our basic sampling units, hereafter sites. Transects were placed randomly within stratified vegetation types. Sampling was carried out each month from March 2005 to August 2006. Spiders were sampled along the transects using pitfall traps and semi-quantitative sampling. Pitfall sampling was operated for 64 weeks and other semi-quantitative sampling performed on 64 occasions (once every week) at the same sampling sites. The principal purpose of this sampling design was to produce a relatively complete species list and associated abundance data for a representative example of each vegetation type in the region, and of the region as a whole.

Pitfall sampling: Pitfall traps consisted of cylindrical plastic bottles of 10 cm diameter and 11 cm depth (Churchill & Arthur 1999). Six pitfall traps were laid along each transect line at an interval of 10 m each. Traps were filled with preservative (69% water, 30% ethyl acetate, and 1% detergent). After seven days, specimens were removed from traps, which allowed us to maintain spider specimens in good condition before laboratory processing and identification. Since the limitations of this method are that the number of individuals trapped is affected by environmental, weather and species-specific factors (Mitchell 1963; Ahearn 1971; Parmenter et al. 1989; Krasnov & Shenbrot 1996), we have employed other time constrained semi-quantitative collection methods after Coddington et al. (1996) to maximize capture.

Semi-quantitative sampling: Aerial sampling (for upper layer spiders up to 1.5 m) involved searching leaves, branches, tree trunks, and spaces in between, from knee height up to a maximum overhead arm's reach. Ground collection (for ground layer spiders) involved searching on hands and knees, exploring the leaf litter, logs, rocks, and plants below low knee level. Beating (for middle layer spiders up to 1 m) consisted of striking vegetation with a 1 m long stick and catching the falling spiders on a tray held horizontally below the vegetation. Litter sampling was done by hand sorting spiders from leaf litter collected in a litter collection tray. Sweep netting (for middle layer spiders up to 1 m) was carried out in order to access foliage dwelling spiders. Each sampling method comprised 1 hour active sampling, measured with a stopwatch.

Spiders were identified to family and species using existing identification keys wherever possible (Pocock 1900; Tikader & Malhotra 1980; Tikader 1982, 1987; Koh 2000; Cushing 2001). Due to lack of available identification keys for many families and the time required for conventional taxonomic work, a morphospecies approach was used to classify spiders. This approach has been found to be effective for poorly known and species-rich taxa such as spiders and other invertebrates (Oliver & Beattie 1996; Krell 2004). Voucher specimens of each spider species collected are deposited at the Wildlife Institute of India, Dehradun and will ultimately be placed in the Arachnida Section, Zoological Survey of India, Kolkata.

Based on hunting methods and web building types from the literature (Uetz et al. 1999; Höfer & Brescovits 2001), combined with field observations, we grouped the spider families of Terai into the following five major guilds: 1) orb weavers: Araneidae, Tetragnathidae, and Uloboridae; 2) space weavers: Pholcidae and Theridiidae; 3) ground weavers: Hahniidae, Linyphiidae, Agelenidae, and Theraphosidae; 4) foliage runners: Clubionidae, Oxyopidae, Philodromidae,

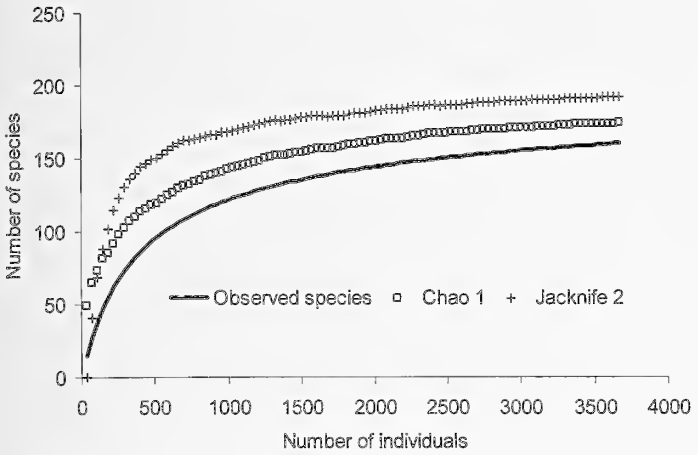

Figure 1.—Species-accumulation curve and estimation curves Chao1 and Jacknife2 for the regional (all samples pooled) dataset. Curves are generated from 100 randomizations.

Pisauridae, Scytodidae, Sparassidae, Salticidae, and Thomisidae; 5) ground runners: Lycosidae, Gnaphosidae, Oonopidae, Zodariidae, and Tetrablemmidae.

Data Analysis.—Spiders captured by pitfall traps and semiquantitative methods were pooled for each site. Species richness was estimated for each vegetation type, as well as for the regional data set using the nonparametric estimators Chao1 and Jacknife2. Accumulation curves were generated after 100 randomizations using EstimateS 8.0 © (Colwell 2006). Chao1 gives an estimate of the absolute number of species in an assemblage based on the number of rare species (singletons and doubletons) in a sample. Chao1 estimate of species richness is recommended for inventory completeness values, completeness being the ratio between observed and estimated richness (Sørensen et al. 2002; Scharff et al. 2003). Jacknife estimators in general, and Jacknife2 in particular, have been found to perform quite well in extrapolation of species richness with greater precision, less bias, and less dependence on sample size than other estimators (Palmer 1990, 1991; Baltanás 1992; Brose et al. 2003; Petersen et al. 2003; Chiarucci et al. 2003). To compare the species richness values of sites and to calculate expected species richness, individual-based rarefaction was used (Gotelli & Colwell 2001). These curves standardize different datasets on the basis of number of individuals and not on number of samples. The software program EcoSim7.0 (Gotelli & Entsminger 2001) was used for rarefaction analyses. Thereafter, the curves were rarefied to the lowest number of individuals recorded in a vegetation type (300) to ensure valid comparisons of species richness between different sites (Gotelli & Colwell 2001). Rarefaction was used as a diversity index because it considers the number of individuals collected and species richness (Magurran 2004), allows comparison of diversity between sites at similar sample size, and by showing the rate of new species accumulation, allows for verification that enough samples were collected to make proper comparisons of diversity (Gotelli & Colwell 2001; Magurran 2004; Buddle et al. 2005).

The similarity across sites was depicted as Bray-Curtis similarities (Krebs 1989), using both species and guild composition. Multidimensional scaling (MDS) plots were constructed based upon similarity values of species composition across vegetation types in program PRIMER (Clarke & Gorley 2001). Analysis of similarities (ANOSIM – Clarke 1993) was performed between each pair of vegetation types to determine whether there were significant differences between the spider assemblages in the five main vegetation types. The data were fourth-root transformed before analysis to reduce the weight of common species (Clarke & Warwick 1994). The ANOSIM procedure of PRIMER is a nonparametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993). This method generates a global R-statistic, which is a measure of the distance between groups. An R-value that approaches one indicates strongly distinct assemblages, whereas an R-value close to zero indicates that the assemblages are barely separable (Clarke 1993). These R-values were used to compare spider assemblages between vegetation types. Where ANOSIM revealed significant differences between groups, SIMPER analyses (PRIMER) were used to identify those species that contributed most to the observed assemblage differences (Clarke & Gorley 2001). Similarity percentages (SIMPER) allowed identification of species and guilds important in discriminating between groups that differed significantly from each other. Cumulative contributions were cut arbitrarily at 50%. The species with the highest dissimilarity to standard deviation ratios were identified as good discriminators for each comparison (Clarke 1993).

RESULTS

Comparison of community structure between vegetation types.—We captured a total of 3666 adult spiders representing 22 families, 60 genera, and 160 species, which represent 11% of spider species recorded on the Indian mainland (Siliwal et al. 2005). The pooled species accumulation curve reached an asymptote for both Chao1 and Jacknife 2 (Fig. 1), indicating

Table 1.—Measures of species richness estimates and inventory completeness for each vegetation type and for the regional dataset. Richness estimator values (Chao1 & Jacknife2) represent the mean of 100 randomizations of sample order. Ratio of estimated and observed richness represents inventory completeness. All values rounded to the nearest integer.

	Pure Sal Woodland	Mixed Sal Woodland	Plantation	Grassland	Riparian Swamp Forest	Regional
No. of specimens	777	805	301	729	1054	3666
Observed richness	87	76	41	76	95	160
Number of singletons	19	18	8	13	28	35
Number of doubletons	11	7	5	3	10	13
Chao1	103	99	73	135	127	173
Jacknife2	108	98	60	99	136	191
% Completeness	84	77	56	56	75	92

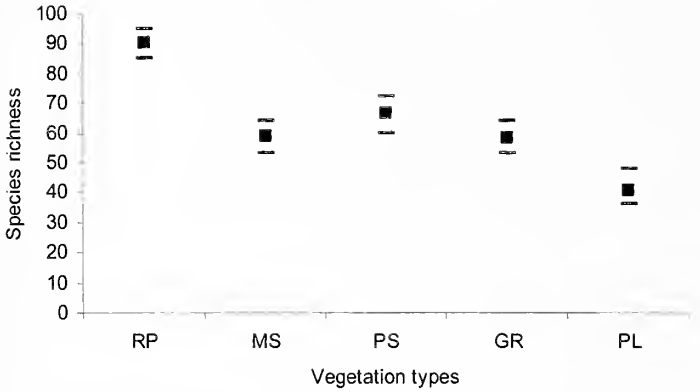

Figure 2.—Comparison of species richness values (± 95% confidence interval) at the lowest number of individuals (300) derived from individual-based species rarefaction curves of spider assemblages across the different vegetation types. RP, Riparian; MS, Mixed Sal; PS, Pure Sal; GR, Grassland; PL, Plantation.

that sampling was almost complete at the regional level. The estimated total species richness using Chao1 was 173 ± 8.32 (SD), and using Jacknife2 191 ± 1.82 (SD) for the complete sample. The ratio of observed to estimated (Chao1) number of species was 92% suggesting that at least 8% more species are to be expected in the area than were actually collected. However, at a local level, in plantation and grassland, we failed to collect such a high percentage of species (44% missing) compared with other vegetation types (Table 1). The most abundant families were Araneidae (41.78% of all captures), and Theridiidae (12.46%). Other dominant families comprised Lycosidae (295 individuals, 11 species), Tetragnathidae (253, 17), Linyphiidae (211, 19), Clubionidae (170, 4), Salticidae (133, 12), and Gnaphosidae (123, 7). All other families (14) were represented by less than 100 individuals each, and contributed only 29 species. From all species recorded, 35 were singletons (21% of all species) and 13 were doubletons (8% of all species). The most abundant species was *Chrysso picturata* Simon 1895 (Theridiidae) (112 individuals) and most of the individuals (70% of total catches) were found at plantation sites. The highest species richness was found in the riparian swamp forest (90 species), while the lowest species richness was in the plantation sites (41 species). The remaining three vegetation types did not differ statistically in richness considering the overlap of confidence intervals of richness values (Fig. 2).

Comparison of species composition between sites and vegetation types.—Comparing among different sites revealed that on average, species composition was much more similar within the same vegetation type than among different vegetation types. MDS plot generated from relative abundances of different spider species in each vegetation type showed that sampling sites from each vegetation type clustered together (Fig. 3a). Sampling sites of homogeneous grassland and plantation were well separated from heterogeneous forest habitats, which clustered together. Sampling sites in pure sal and mixed sal woodland grouped together and showed little overlap with other vegetation types. Pair wise ANOSIM test showed that most difference in species composition occurred between riparian swamp forest and plantation sites ($R = 0.79$, $P = 0.001$), while the least difference was seen between pure

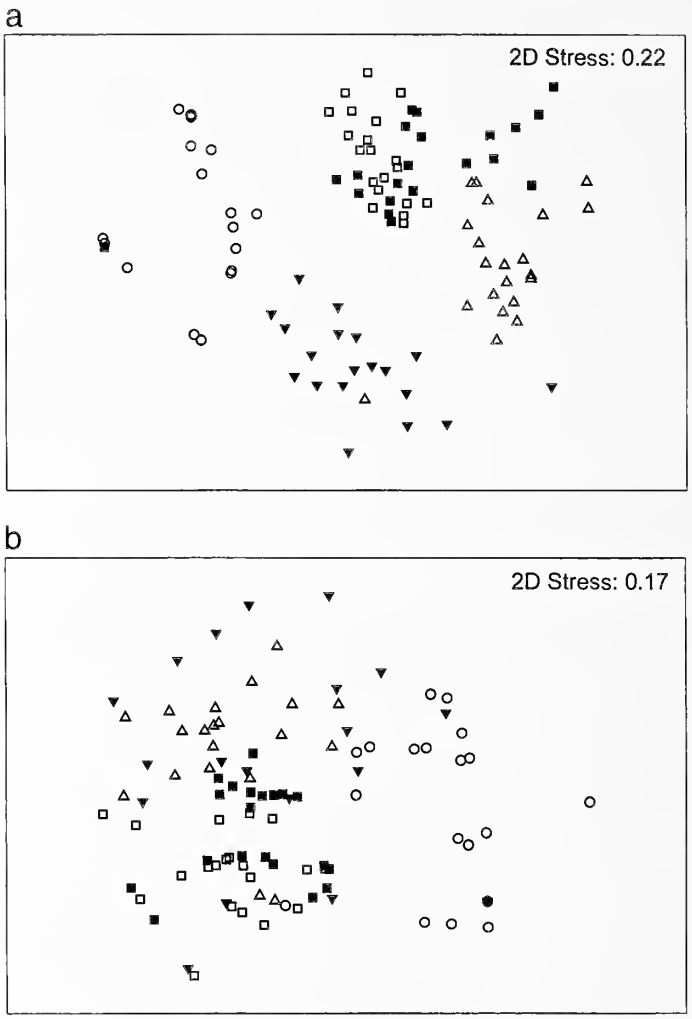

Figure 3.—MDS ordination plots of sampling plots in the Terai Conservation Area, generated by (a) species composition and (b) guild composition, sorted according to vegetation types (open triangle, Riparian sites; inverted closed triangle, Grassland sites; open square, Pure Sal sites; closed square, Mixed Sal sites; open circle, Plantation sites).

sal and mixed sal woodland ($R = 0.34$, $P = 0.011$). Further comparisons of dissimilarity in composition were made to identify the species contributing to the difference between groups of sites that differed most. Fifteen species contributed more than 50% to the difference between groups of sites. These species differed in mean abundance, which was reflected in the degree of group association. Eight species of family Araneidae, were almost absent from plantation sites and present in high abundance in riparian swamp forest, whereas *Chrysso picturata* and *Argyrodes* sp. 2 of family Theridiidae were found in greater abundance at plantation sites compared to riparian forest (Table 2a).

Comparison of guild between sites and vegetation types.—A MDS plot generated for relative abundances of different spider guilds showed distinct patterns with respect to the five vegetation types (Fig. 3b) and statistically significant differences ($R = 0.75$–0.21, $P < 0.001$) revealed by all pair-wise ANOSIM tests except pure sal vs. mixed sal ($R = 0.096$, $P = 0.19$). SIMPER analysis indicated that the orb weaver guild was the main contributor to dissimilarity between riparian

Table 2.—SIMPER analysis of differences in (a) species (average dissimilarity = 94.95%) and (b) guild (average dissimilarity = 50.00%) composition of spider assemblages between the two most dissimilar vegetation types studied.

		Vegetation type		
		Riparian	Plantation	
	Family	Mean abundance	Mean abundance	Cumulative contribution%
(a) Species				
Argiope pulchella (Thorell, 1881)	Araneidae	0.94	0.00	4.57
Chrysso picturata (Simon, 1895)	Theridiidae	0.06	0.82	8.80
Gasteracantha sp. 1	Araneidae	0.86	0.00	12.99
Gasteracantha dalyi (Pocock, 1900)	Araneidae	0.86	0.00	17.18
Hippasa sp. 3	Lycosidae	0.80	0.00	21.13
Eriovixia excelsa (Simon, 1889)	Gnaphosidae	0.39	0.67	24.54
Achaearanea sp. 2	Theridiidae	0.62	0.56	27.86
Neoscona mukerjei (Tikader, 1980)	Araneidae	0.66	0.00	31.14
Cyphalonotus sp. 1	Araneidae	0.64	0.00	34.17
Neoscona vigilans (Blackwell, 1865)	Araneidae	0.52	0.00	37.14
Myrmarachne sp. 1	Salticidae	0.62	0.00	40.00
Pardosa birmanica (Simon, 1884)	Lycosidae	0.57	0.00	42.79
Argyrodes sp. 2	Theridiidae	0.00	0.52	45.48
Neoscona biswasi (Bhandari & Gajbe, 2001)	Araneidae	0.58	0.00	48.03
Leucauge decorate (Blackwell, 1864)	Tetragnathidae	0.48	0.00	50.41
Araneus bilunifer (Pocock, 1900)	Araneidae	0.46	0.00	52.69
(b) Guilds				
Orb-weavers		5.10	1.57	48.49
Ground runners		3.09	0.69	82.29
Space weavers		1.79	2.62	100.00

swamp and plantation (Table 2b). Orb weaver was the dominant guild with the highest number of individuals (55% of total capture) and was abundant in all vegetation types except plantations (Fig. 4). Colleetively in pure sal and mixed sal, 56% of total orb weavers were captured. Space weavers and foliage runners represented 13% and 12% respectively, while ground runners and ground weavers collectively contributed 12% of all collection.

DISCUSSION

The present study, an inventory of spiders, is the first of its kind in Terai and is one of the few studies on spider communities in India. As there is no species list available for TCA, it is difficult to know precisely what proportion of the actual local and regional species richness our study captured. However, based on estimated richness our inventory was almost complete at the regional scale (92%). In spite of the relative suecess of this study, it still cannot be described as comprehensive – undoubtedly species were missed at local scales. Sampling additional sites or using different methods would capture more species. Nevertheless, the inventory protocol utilized here provided a sufficiently thorough sample of local and regional spider species to permit an accurate comparison of species richness of different vegetation types. The community structure and spider diversity is not similar in different vegetation types. Comparatively, riparian swamp forests exhibit highly diverse assemblages, possibly due to higher struetural complexity. The relatively open and diverse overstorey and understorey structure of riparian swamp forest supported the highest number of spider species while closed canopy woodland and plantation sites supported relatively few (Fig. 5). Additionally, these swamp forests are subjected to annual flooding, which may "reset" areas to earlier successional stages due to removal of existing substrate, organic matter, and organisms, and the deposition of sediments (Junk et al. 1989; Sparks et al. 1990; Richards et al. 2002). These processes may affect spider communities by alteration of microhabitats and their relative availability. The disturbances of successive floods are cumulative, and may lead to a highly heterogeneous patchy habitat condition. However, it is unclear whether such flooding may create higher species richness through removal of dominant species and creation of ecological space for other opportunist species, or through creation of diverse microhabitats, or a combination of these. Intriguingly, our results showed high species richness and diverse assemblage in grassland, considering the low structural diversity of this vegetation type. One of the possible reasons for this pattern may be the practice of annual, low intensity prescribed burning in the grassland. Burning is a management tool used to reduce fuel levels and facilitate regeneration of desired grass species for wild ungulate communities. This annual fire essentially increases structural complexity of grassland, where characteristic elements of both sparse and dense vegetation occur in close proximity, providing a rich mosaic of microclimatic conditions, capable of supporting a large number of spider species (Moretti et al. 2002). However, it would be interesting to observe what proportion of locally and regionally endemic or restricted species are affected negatively or positively by this practice. The spider composition in plantation showed the most dissimilar assemblage in comparison with those of other vegetation types. Possible reasons may be the scarcity of understorey vegetation, single tree species dominance, and isolation from nearest forest habitat, affecting the amount of different microhabitats

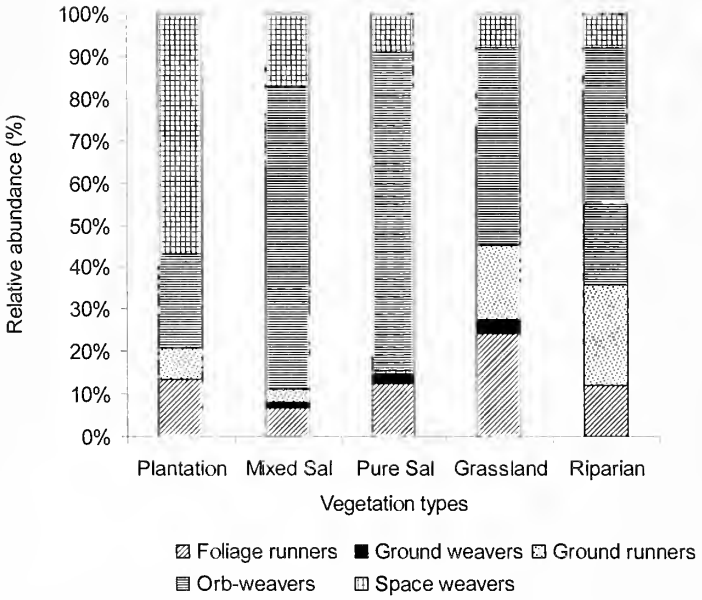

Figure 4.—Variation in guild structure of spider assemblages across different vegetation types in the Terai Conservation Area.

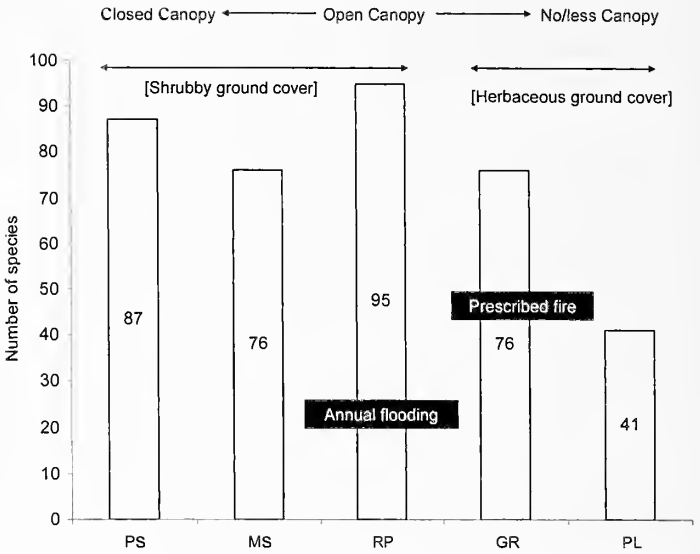

Figure 5.—Patterns of species richness of spider assemblages across vegetation types showing some gross ecological features shared among vegetation types in Terai. Arrows indicate gradient of ecological characteristics, brackets indicate features common to vegetation types. RP, Riparian; MS, Mixed Sal; PS, Pure Sal; GR, Grassland; PL, Plantation.

available to spiders. Patch isolation can act as a barrier to spider dispersal from other patches. Bonte et al. (2004) showed that the distribution of spider species depends on their aerial dispersal potential and on habitat connectivity. Plantations had higher abundance of space weavers and relatively few orb weavers. This pattern probably resulted from lack of suitable microhabitats for orb web construction (vegetation dominated by a few species of dense and short grasses, with low densities of herbaceous ground flora), as well as exposure to wind and rain due to relatively open canopy. Compared with orb weavers, space weavers can endure a higher level of disturbance, which may explain why they are more abundant (Tsai et al. 2006). In contrast, relative abundance of orb weavers was much higher in pure sal and mixed sal woodland, where dense canopy and stable microclimate prevails year round. These habitats have high vertical stratification (Robinson 1981; Scheidler 1990; Balfour & Rypstra 1998) and may offer more physical structures for web attachment, such as different kinds of branches. Such variation in species abundance of orb weavers can potentially be used to monitor changes of structural quality of vegetation parameters and habitat disturbances. However, serious lack of ecological and taxonomic understanding of Indian spiders hinders their use as indicators of habitat disturbance in India (Kapoor 2008). On a coarse scale, this study revealed the relative importance of habitat type on diversity and composition of spider assemblage in TCA. However, future studies need to quantify habitat characteristics, microclimate variability and disturbance factors in order to depict how these features affect community structure and composition and in what way they are correlated with species diversity at local as well as regional scales.

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First record of the scorpion genus *Microtityus* from Colombia, with the description of a new species (Scorpiones, Buthidae)

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Abstract. *Microtityus (Microtityus) franckei* sp. nov. is described from both male and female specimens from the transition zone of the Tayrona Natural National Park, located in the Caribbean region of Colombia. The new species, which is the first of the genus reported from Colombia, is characterized, among other features, by reductive neobothriotaxy on the pedipalp femur and chela. The new species raises to 25 the number of known species of *Microtityus*, ten of which are present in continental South America. A revised diagnosis of the genus, a species check-list, and some biogeographic and taxonomic considerations are included.

Keywords: Scorpions, taxonomy, Tayrona Natural National Park

The genus *Microtityus* Kjellesvig-Waering 1966 is a group of scorpions including 24 known species (one fossil) and two subspecies (Armas 1999; Fet & Lowe 2000; Teruel 2000, 2001; González-Sponga 2001; Teruel & Armas 2006; Teruel & Infante 2007). The genus is known mainly from the Caribbean islands, with seven species present in Cuba, five in the Dominican Republic, one in Trinidad and Tobago, and one in the U.S. Virgin Islands—St. Thomas and St. John Islands (Francke & Sissom 1980; Armas 1999; Fet & Lowe 2000; Teruel 2000, 2001; Teruel & Armas 2006; Teruel & Infante 2007). Even though Armas (1974:24) mentioned the presence of this genus in Puerto Rico (according to a personal communication from M.A. González-Sponga), no species from that island is known to date. Similarly, although Santiago-Blay et al. (1990) made reference to the genus in Haiti, they did not mention the specific identity of populations from that country, and no paper stating the presence of any species of *Microtityus* in Haiti has yet been published. In continental South America this genus is represented by a lower number of species; eight from Venezuela and only one from Brazil (Fet & Lowe 2000; González-Sponga 2001).

Armas (1974) created the subgenus *Microtityus* (*Parvabsonus*) for the Cuban species *Microtityus fundorai* Armas 1974, *Microtityus jaumei* Armas 1974 and *Microtityus trinitensis* Armas 1974, and 13 species from Caribbean islands have been described in the subgenus. More recently, Teruel (2000) defined two species-groups within *Microtityus* (*Parvabsonus*) to separate the species with reductive neobothriotaxy (*M. jaumei* group: femoral trichobothrium d_2 absent) from those with orthobothriotaxy (*Microtityus waeringi* Francke & Sissom 1980 group: femur with the complete set of trichobothria). Even though the remaining species are placed within the nominal subgenus, their subgeneric position should be reevaluated—as has already been indicated by Fet & Lowe (2000). A check-list of the species and the countries where they are known to occur as well as the current subgeneric and species-group placements are presented in Table 1. *Microtityus starri* Lourenço & Huber 1999 and *Microtityus iviei* Armas 1999 are not included in the table since Prendini (2001) synonymized the former species with *Microtityus rickyi* Kjellesvig-Waering 1966, and Teruel (2005) considered the second an invalid taxon.

The relatively high species richness of this genus in Venezuela contrasts strongly with neighboring countries such as Brazil with a single species, and Colombia and Guyana where *Microtityus* is unrecorded. Despite this situation, recent collections carried out by the second author at the transition zone of the Tayrona Natural National Park (Fig. 1) discovered a new population of *Microtityus* that corresponds to a new species that is herein described and assigned to the nominal subgenus. The new species is the first of the genus to be known from Colombia, raising to five the number of buthid genera in the country: *Ananteris* Thorell 1891, *Centruroides* Marx 1890, *Microtityus*, *Rhopalurus* Thorell 1876 and *Tityus* Koch 1836.

METHODS

Photographs were taken using an Olympus D-590 ZOOM digital camera. Illustrations were prepared with the aid of a *camera lucida* mounted onto a Zeiss Stemi SV 6 stereoscope. Measurements (L = length, W = width, D = depth) are presented in millimeters and were obtained following the methodology of Sissom et al. (1990) using the program Motic Images 2000 version 1.2 through a PC connected to a Motic Digital Microscope DM-143. The distribution map was produced with the program ArcView GIS version 3.1 (Environmental Systems Research Institute (ESRI), Redlands, California). All specimens are preserved in 70% ethanol.

General carinal terminology follows Vachon (1952), except for the mesosomal carinae that are here distinguished as follows. In the tergites: axial, dorsolateral and lateral carinae; in the sternites: paramedian and lateral carinae. According to Vachon's (1952) terminology for the carinae on the pedipalp femur, the carina that follows the dorsointernal is referred to as ventrointernal (see Vachon 1952:fig. 65); however, in the specimens studied herein there is an additional and more ventral carina to which the term ventrointernal is more suitable, thus making it necessary to replace Vachon's (1952) term ventrointernal for internal median. Trichobothrial terminology follows Vachon (1973, 1975). In the present paper, the notion of subgenus is used as an optional rather than obligatory category.

Table 1.—Checklist of the species of *Microtityus* and the countries where they have been reported. Species marked with single asterisk (*) belong to the *M. waeringi* species-group while those with double asterisk (**) belong to the *M. jaumei* group according to Teruel's (2000) proposal.

Species	Brazil	Colombia	Cuba	Dominican Republic	Trinidad and Tobago	Venezuela	U. S. Virgin Islands
M. (Microtityus) anbarensis (Schawaller 1982) (fossil)				X			
M. (Microtityus) angelaerrosae González-Sponga 2001						X	
M. (Microtityus) biordi González-Sponga 1970						X	
M. (Microtityus) capayaeusis González-Sponga 2001						X	
M. (Microtityus) desuzei González-Sponga 2001						X	
M. (Microtityus) franckei		X					
M. (Microtityus) joseantonioi González-Sponga 1981						X	
M. (Microtityus) litoralensis González-Sponga 2001						X	
M. (Microtityus) rickyi Kjellesvig-Waering 1966					X		
M. (Microtityus) sevciki González-Sponga 2001						X	
M. (Microtityus) vanzolinii Lourenço & Eickstedt 1983	X						
M. (Microtityus) yaracuyanus González-Sponga 2001						X	
M. (Parvabsonus) consuelo Armas & Marcano-Fondeur 1987 *				X			
M. (Parvabsonus) difficilis Teruel & Armas 2006 **			X				
M. (Parvabsonus) dominicanensis Santiago-Blay 1985 *				X			
M. (Parvabsonus) farleyi Teruel 2000 *			X				
M. (Parvabsonus) fundorai Armas 1974 **			X				
M. (Parvabsonus) guantanamo Armas 1984 *			X				
M. (Parvabsonus) jaumei Armas 1974 **			X				
M. (Parvabsonus) kovariki Teruel & Infante 2007 **			X				
M. (Parvabsonus) lantiguai Armas & Marcano-Fondeur 1992 *				X			
M. (Parvabsonus) paucidentatus Armas & Marcano-Fondeur 1992 **				X			
M. (Parvabsonus) trinitensis Armas 1974 **			X				
M. (Parvabsonus) virginiae Armas 1999 *				X			
M. (Parvabsonus) waeringi Francke & Sissom 1980 *							X

Acronyms of museums: Museo Javeriano de Historia Natural "Lorenzo Uribe S. J.," Pontificia Universidad Javeriana, Bogotá, Colombia (MPUJ); Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia (ICN-MHN).

TAXONOMY

Family Buthidae Koch 1837
Genus *Microtityus* Kjellesvig-Waering 1966

Microtityus Kjellesvig-Waering 1966:130.

Type species.—*Microtityus rickyi* Kjellesvig-Waering 1966 by original description.

Revised diagnosis.—Very small scorpions (less than 25 mm length); general coloration yellowish to reddish-yellow with variegated pigmentation; carapace sub-triangular and emarginated, with three pairs of lateral eyes; pedipalps either orthobothriotaxic [11 trichobothria on femur in A-α configuration, 13 on patella and 15 on chela: subgenus *Microtityus* (*Parvabsonus*) (in part, only *M. waeringi* group), subgenus *Microtityus* (*Microtityus*) (in part)], with only femur neobothriotaxic [trichobothrium d_2 absent: *Microtityus* (*Parvabsonus*) (in part, only *M. jaumei* group), *Microtityus* (*Microtityus*) (in part)], with both femur and chela neobothriotaxic [*Microtityus* (*Microtityus*) (in part)], or with only chela neobothriotaxic [*Microtityus* (*Microtityus*) (in part, only *Microtityus litoralensis* Gonzaléz-Sponga 2001)]; dentate margin of pedipalp movable fingers composed of 9–12 oblique rows of granules, without accessory granules; tergites with three or five longitudinal carinae; pectines with well developed fulcra; sternum sub-pentagonal; booklung spiracles ovoid; subaculear tubercle strong and rhomboidal.

Microtityus (*Microtityus*) *franckei* sp. nov.
Figs. 1–14; Tables 1–3

Type material.—*Holotype:* COLOMBIA: *Department of Magdalena*: adult female, Santa Marta, transition zone of the Tayrona Natural National Park, Kalache Kalabria private reserve, 11°16′21″N, 74°04′59.9″W, December 2006, J.A. Noriega (MPUJ-SCO-366).

Paratypes: COLOMBIA: *Department of Magdalena*: 2 adult males, collected with holotype (MPUJ-SCO-367, ICN-MHN-As-650).

Etymology.—The species name is a patronym dedicated to Oscar F. Francke, arachnologist at the Universidad Nacional Autónoma de México, in recognition of his many contributions to scorpiology and acknowledgment of his advice in the senior author's research.

Diagnosis.—The new species seems to be most closely related to both *Microtityus joseantonioi* González-Sponga 1981 and *Microtityus desuzei* González-Sponga 2001 from Venezuela, with which it shares the presence of only 10

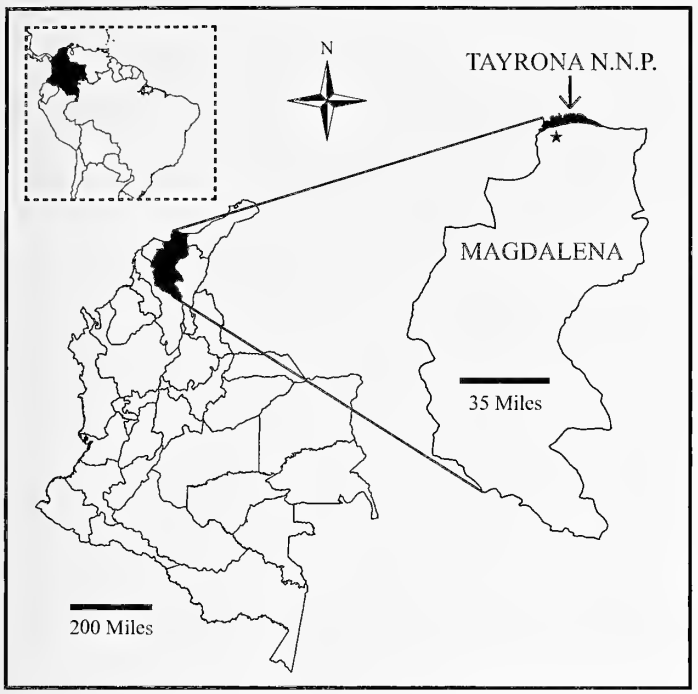


Figure 1.—Location of the type locality of *Microtityus franckei* sp. nov.

trichobothria on the pedipalp femur (d_2 absent) and 12 on the chela (Eb_3, *Esb* and *esb* absent) (Figs. 9, 10, 13, 14; Table 2), rather than the standard pattern of 11 and 15 trichobothria on both segments, respectively. *Microtityus franckei* can be readily distinguished from both species of the neighboring country because it bears 11–12 rows of granules in the movable finger of pedipalps, the internal tubercle on the base of pedipalp femur is low and non-spinoid in both sexes (Figs. 9, 10), and sternite V of males exhibits only one hyaline and smooth area, which is shaped like an equilateral triangle (Fig. 8). In contrast, judging from the original descriptions, in *M. joseantonioi* and *M. desuzei* the movable finger presents 9 rows of granules, the internal tubercle on the base of the pedipalp femur is pronounced and spinoid (González-Sponga 1981:fig. 11; González-Sponga 2001:fig. 7), and sternite V of males exhibits 3 hyaline and smooth areas (González-Sponga 1981, 2001) of which the median one is higher than wide in *M. joseantonioi* (González-Sponga 1981:fig. 14). The new species may be also distinguished from *M. desuzei* in that it presents five carinae in tergites I–VII, rather than only three as in the second species (González-Sponga 2001).

Description of the female holotype (MPUJ-SCO-366).—Measurements in Table 3. *Coloration:* carapace predominantly yellow with abundant dark-brown mottling. Median ocular tubercle dark-brown. Chelicerae yellow with some brownish areas located basally on both fixed and movable fingers, and one externally on tibia; teeth reddish. Tergites almost completely yellow; I–IV with brown regions restricted to the posterior margin and separated from each other by the longitudinal carinae; V–VII with few, disperse brown spots. Coxosternal region with all the components yellowish, with abundant brown spots that are darker in coxapophyses II and are fused in a great brown area obscuring coxapophyses I almost completely. Genital operculum yellow with a small brown area located laterally on each piece. Basal piece of the basal lamellae of the pectines with few spots; the remaining pieces and the pectinal basal piece completely yellow. Sternites with few dark-brown spots. Metasoma yellowish with brown mottling throughout. Telson predominantly yellow, brownish basally near the dorsal surface; body of the subaculear tubercle and distal area of the vesicle brown, margins of the subaculear tubercle yellow; aculeus dark-red over almost its entire length, yellow basally. Pedipalps with variegated pigmentation over dorsal, internal, and external surfaces of all segments, ventral surfaces completely yellow; fixed and movable fingers brown-colored basally and yellow over the rest of their lengths. Legs with variegated pigmentation in all segments.

Carapace: subtriangular, densely granulose throughout; anterior margin moderately emarginated; median ocular tubercle slightly anterior to the center of the carapace; lateral ocular tubercles each with three ocelli; median ocular and posterior median carinae granulose and moderately strong; other carinae and furrows inconspicuous.

Chelicerae: with abundant setae on internal and ventral surfaces; cheliceral dentition characteristic of the family Buthidae (Vachon 1963). Movable finger externally with two small basal teeth, one median pronounced, one subdistal slightly shorter than the median, and one distal tooth. Internally with two small teeth, one basal and one median, and one distal tooth that is longer than its external counterpart. Fixed finger externally with one basal and one median tooth mounted onto a bicuspid, one subdistal, and one distal tooth. Internally with only one small tooth located slightly basal in respect to the external subdistal.

Coxosternal region: sternum pentagonal with a deep median depression; all the components of this region granulose; coxapophyses I–II anteriorly with dense pilosity.

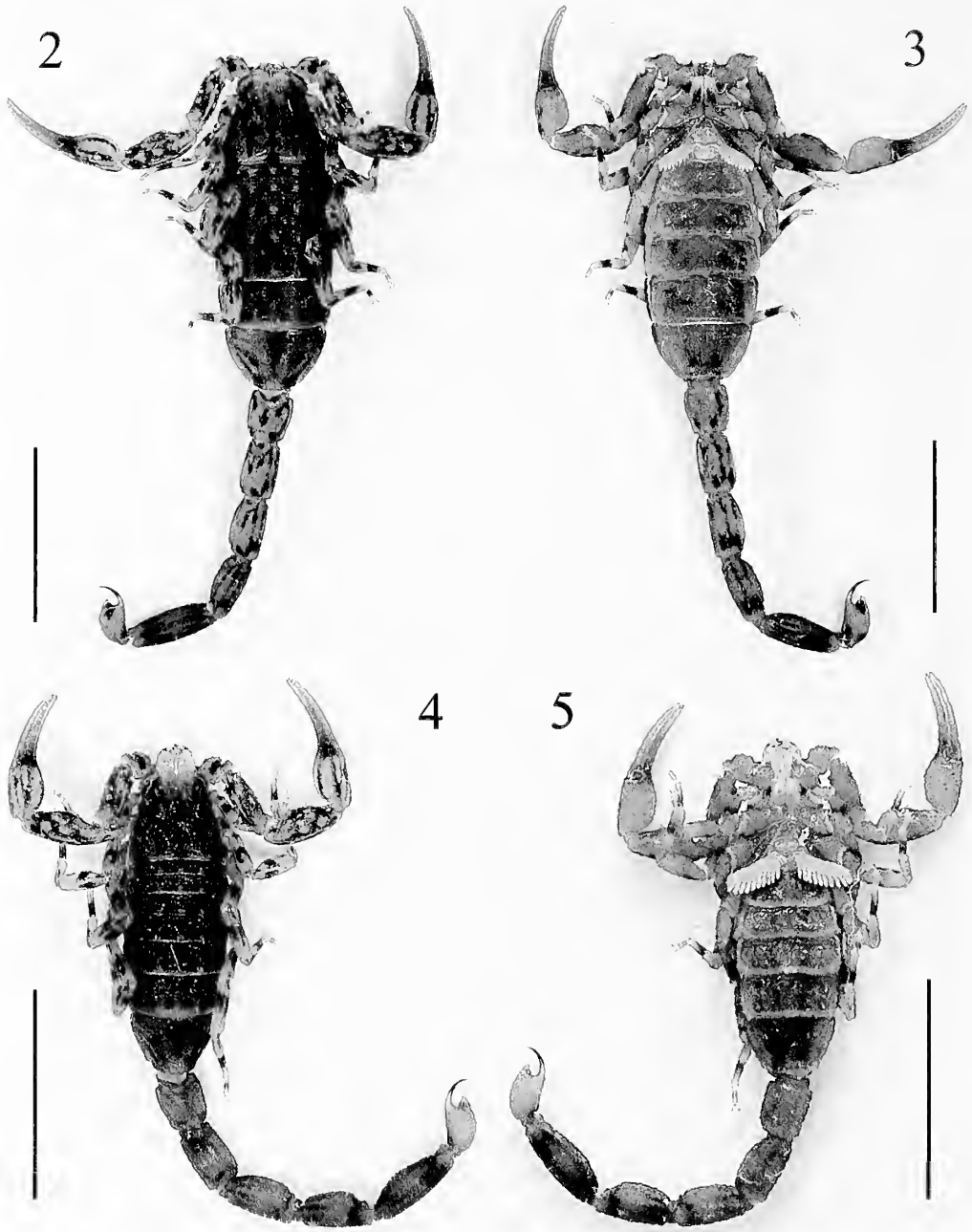
Tergites: with similar granulation to that of the carapace; five longitudinal carinae (axial, paired dorsolateral and lateral carinae) are present on the posterior half of tergites I–VI and are formed by elevated granules that are arranged linearly, the posterior most granule on each carina is markedly stronger and surpasses the margin of the tergite; tergite VII pentacarinate.

Genital operculum and pectines: genital operculum divided longitudinally; pieces count on the pectines: basal lamellae 3:3, middle lamellae 6:6, fulcra 7:8, teeth 8:9; pectinal basal piece almost quadrangular in shape, expanded distally and with the posterior margin straight (Fig. 6).

Sternites: densely granulose throughout; sternites VI–VII with paired paramedian and lateral carinae, incomplete and granulose; booklung spiracles short and oval.

Metasoma: segments I–II with ten carinae (paired ventral, ventrolateral, intermedian, dorsolateral and dorsal carinae); segments III–IV with eight (intermedian carinae absent); segment V with five (axial, paired ventrolateral and dorsolateral carinae); all carinae serrulose; intercarinal spaces granulose. Telson with axial carina that terminates in a rhomboidal subaculear tubercle that is curved towards the aculeus and exhibits two small dorsal granules; aculeus strongly curved.

Pedipalps: densely granulose throughout; femur with five longitudinal carinae (dorsoexternal, dorsointernal, ventrointernal, ventroexternal and internal median carinae), and low

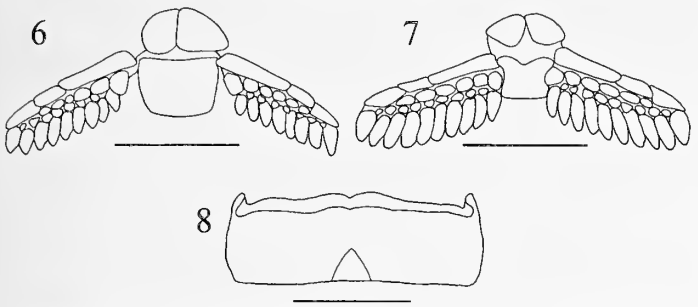


Figures 2–5.—*Microtityus franckei* sp. nov., dorsal and ventral views. 2–3. Female holotype (MPUJ-SCO-366); 4–5. Male paratype (MPUJ-SCO-367). Scale bars equal 5 mm.

and non-spinoid tubercle located basally on the internal surface (Figs. 9, 10); patella with seven longitudinal carinae [all of those identified by Vachon (1952:figs. 66–68) except for the ventral median that is absent], with two spinoid granules on the dorsointernal carina and one in the ventrointernal (Fig. 11); hand with seven longitudinal carinae [all of those identified by Vachon (1952:fig. 69)], of which the dorsal axial, dorsal accessory and intermedian carinae extend over part of the fixed finger; all carinae granulose. Movable fingers with 12 slightly imbricate rows of granules in both pedipalps; fixed fingers with ten rows. Pedipalps neobothriotaxic; trichobothriotaxy Type A, femur with α configuration (Figs. 9–14) (Vachon 1973, 1975); femoral trichobothrium d_2 absent (Fig. 9); patellar d_2 petite and almost indistinguishable (Fig. 11); Eb_3, *Esb* and *esb* absent on chela (Fig. 13).

Legs: tibia, basitarsus and telotarsus with abundant setation; prolateral and retrolateral pedal spurs present on all legs.

Comparisons with male paratypes.—*MPUJ-SCO-367:* Measurements in Table 3. The following features differ from those described for the female holotype: tergites V–VI with similar coloration pattern to the preceding tergites. Coxapophyses II and coxae I–IV completely yellow. Pieces count on the pectines: fulcra 9:9, teeth 10:10. Pectinal basal piece less expanded than the female's and emarginated anteriorly (Fig. 7). Sternite V with a posterior median hyaline and smooth area, which is



Figures 6–8.—*Microtityus franckei* sp. nov. 6–7. Genital operculum, pectines and pectinal basal piece. 6. Female holotype (MPUJ-SCO-366); 7. Male paratype (MPUJ-SCO-367). 8. Sternite V of male paratype (MPUJ-SCO-367). Scale bars equal 1 mm.

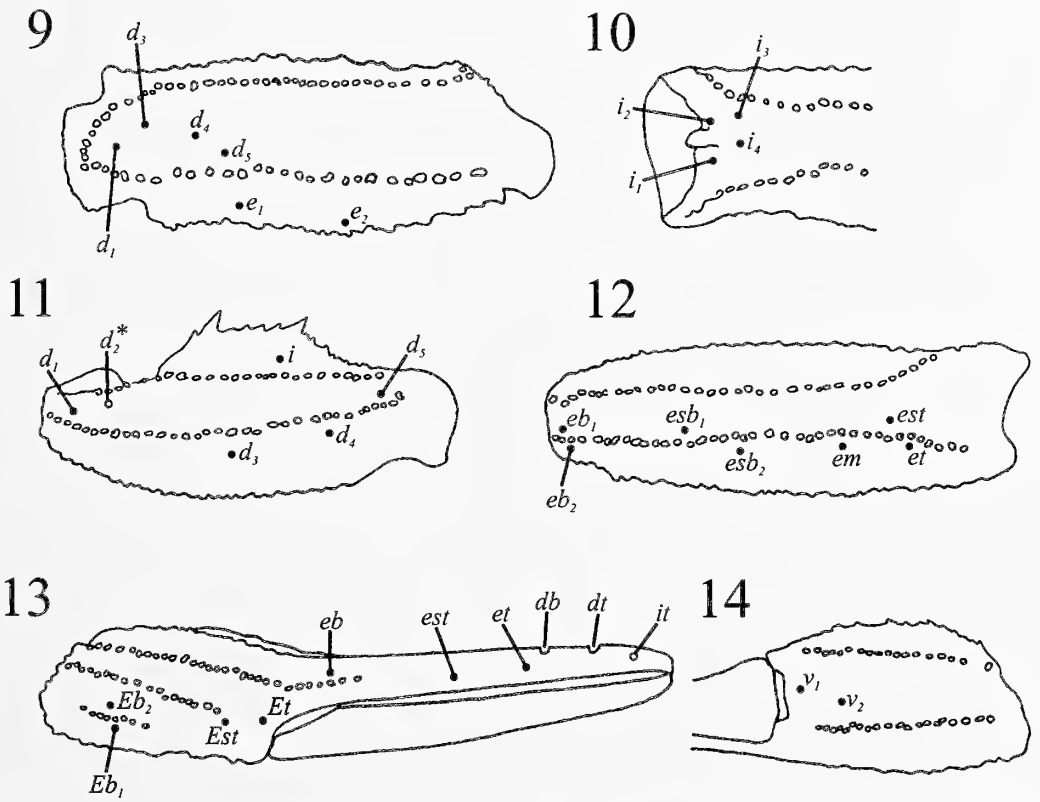
shaped like an equilateral triangle (Fig. 8). Cheliceral dentition identical to that of the female. Pedipalp movable fingers with the same 12 rows of granules of the female.

ICN-MHN-As-650: Measurements in Table 3. Similar to the other male, except that patellar trichobothrium d_2 is absent in both pedipalps, pedipalp patella bears eight longitudinal carinae with ventral median carina present, and the movable fingers present 11:12 rows of granules.

Distribution.—*Microtityus franckei* is known only from the type locality: Kalache Kalabria private reserve at 11°16′21″N, 74°04′59.9″W (Fig. 1). This species inhabits the Santa Marta Montane Forests ecoregion, which rises from very different habitat of xeric scrub and dry forest that surround it. This ecoregion is a mountain massif whose northern edge runs just off the coast of the Caribbean Sea. Due to both plant and animal endemism it is considered a Pleistocene refuge, although its diversity is relatively low and limited in comparison with other Neotropical ecoregions (National Geographic Society 2001).

Field observations and sympatric species.—All of the specimens were hand captured in daylight from under stones in the dry bed of a river at 134 m above sea level. This species was found in sympatry with *Ananteris columbiana* Lourenço 1991, *Tityus tayrona* Lourenço 1991, and an unidentified species of *Chactas* Gervais 1844.

Some biogeographic and taxonomic considerations.—Even though Armas & Marcano-Fondeur (1992) suggested that reductive neobothriotaxy has occurred independently more than once within *Microtityus*, Teruel (2000) rejected such an hypothesis arguing that: (i) the loss of trichobothria is an infrequent phenomenon in the family Buthidae and when it occurs in various species of the same genus, it is a synapomorphic condition; (ii) the *M. jaumei* species-group is a natural lineage that seems to have evolved from an orthobothriotaxic ancestor—an hypothesis supported by the presence of this condition in the most ancient species of the genus known to date, *Microtityus ambarensis* (Schawaller 1982) from Dominican amber of 40–30 mya. Although Teruel's (2000) consideration—which was not backed by a cladistic analysis—seems correct for the Caribbean species of *Microtityus* [subgenus *Microtityus* (*Parvabsonus*)], it appears inappropriate when the continental species are considered since this region is occupied also by both orthobothriotaxic



Figures 9–14.—Distribution of the trichobothria in female holotype *Microtityus franckei* sp. nov. (MPUJ-SCO-366). 9. Femur, dorsoexternal view; 10. Femur, internal view; 11. Patella, dorsointernal view; trichobothrium with * is petite; 12. Patella, external view; 13. Chela, external view; 14. Chela, ventral view.

Table 2.—Trichobothriotaxy of the species currently assigned to *Microtityus* (*Microtityus*). Ortho = Orthobothriotaxic; Neo = Neobothriotaxic. Trichobothria in parentheses are absent.

Species	Femur	Patella	Chela	References
M. ambarensis	Ortho	Ortho	Ortho	Santiago-Blay et al. 1990; Teruel 2000
M. angelaerrosae	Neo (d_2)	Ortho	Neo (*esb*)	González-Sponga 2001
M. biordi	Ortho	Ortho	Ortho	González-Sponga 1970
M. capayaensis	Neo (d_2)	Ortho	Ortho	González-Sponga 2001
M. desuzei	Neo (d_2)	Ortho	Neo (*Eb*$_3$, *Esb*, *esb*)	González-Sponga 2001
M. franckei	Neo (d_2)	Ortho/Neo (d_2)	Neo (*Eb*$_3$, *Esb*, *esb*)	This paper
M. joseantonioi	Neo (d_2)	Ortho	Neo (*Eb*$_3$, *Esb*, *esb*)	González-Sponga 1981
M. litoralensis	Ortho	Ortho	Neo (*Eb*$_3$, *Et*, *esb*)	González-Sponga 2001
M. rickyi	Ortho/Neo (d_2)	Ortho	Ortho	Kjellesvig-Waering 1966; Vachon 1977; Armas 1988; Prendini 2001
M. sevciki	Neo (d_2)	Ortho	Ortho	González-Sponga 2001
M. vanzolinii	Ortho	Ortho	Ortho	Lourenço & Eickstedt 1983
M. yaracuyanus	Neo (d_2)	Ortho	Ortho	González-Sponga 2001

and neobothriotaxic species (Table 2). In contrast to the neobothriotaxy observed in some insular *Microtityus*, which consists of the absence of only femoral trichobothrium d_2, South American representatives exhibit various different types of neobothriotaxy (Table 2). The distributions of both orthobothriotaxic and neobothriotaxic species indicate that the second condition may have appeared independently more than once. We suggest that an orthobothriotaxic ancestor—probably belonging to the nominal subgenus as it is supported by the fossil evidence—passed from South America to the Caribbean lands about 37–35 mya when both plates were in contact (Iturralde-Vinent & MacPhee 1999). Such an ancestor

Table 3.—Morphometric measurements (mm) of female holotype and male paratypes of *Microtityus franckei* sp. nov.

		Female holotype (MPUJ-SCO-366)	Male paratype (MPUJ-SCO-367)	Male paratype (ICN-MHN-As-650)
Total body length (including telson)		18.65	16.33	14.79
Carapace	Length	2.28	1.86	1.95
	Anterior W	1.38	1.07	1.14
	Posterior W	2.72	2.10	2.29
	Ocular diameter	0.13	0.09	0.10
	Interocular distance	0.20	0.18	0.23
Mesosoma	Total L	5.84	4.71	3.20
Metasoma	Total L (including telson)	10.51	9.76	9.64
	Segment I L	1.32	1.18	1.12
	Segment I W	1.25	1.04	1.09
	Segment I D	1.24	0.97	1.01
	Segment II L	1.59	1.46	1.47
	Segment II W	1.04	0.92	0.93
	Segment II D	1.03	0.91	0.90
	Segment III L	1.64	1.54	1.54
	Segment III W	0.98	0.87	0.86
	Segment III D	0.95	0.91	0.87
	Segment IV L	1.66	1.54	1.62
	Segment IV W	0.90	0.81	0.86
	Segment IV D	0.87	0.86	0.86
	Segment V L	2.43	2.37	2.20
	Segment V W	0.78	0.79	0.80
	Segment V D	0.85	0.87	0.86
	Telson L	1.89	1.67	1.69
	Vesicle W	0.74	0.70	0.65
	Vesicle D	0.77	0.68	0.69
Pedipalps	Total L	7.72	7.72	6.41
	Femur L	1.83	1.48	1.58
	Femur W	0.63	0.55	0.58
	Patella L	2.17	1.75	1.82
	Patella W	0.91	0.69	0.74
	Chela L	3.72	3.05	3.01
	Chela W	0.89	0.79	0.79
	Chela D	0.86	0.74	0.73
	Movable finger L	2.46	1.88	1.92

may then have originated the first form of *Microtityus* (*Parvabsonus*) from which both the *M. jaumei* and the *M. waeringi* groups evolved and diversified. In South America, actual neobothriotaxic species may have evolved, too, from orthobothriotaxic ancestors. These hypotheses await rigorous testing with cladistic analyses, as is the monophyly of *Microtityus* (*Parvabsonus*). Considering that only *M. joseantonioi*, *M. desuzei*, and *M. franckei* share the same trichobothrial pattern it is plausible that these species may be closely related phylogenetically.

Taking into account that Venezuela exhibits a high species richness for this genus in comparison to Colombia, the discovery of *M. franckei* suggests that more species of *Microtityus* may be present in Colombia. This also takes into account one described species exists in the state of Amazonas, Brazil – namely *Microtityus vanzolinii* Lourenço & Eickstedt 1983, plus an additional species from the state of Matto Grosso, partly illustrated by González-Sponga (2001: fig. 23), which yet remains undescribed.

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How many species of fossil arachnids are there?

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Abstract. The species-level diversity of fossil Chelicerata is summarized for each order. 1952 valid species of fossil chelicerates are currently recognized, of which 1593 are arachnids. In order of abundance they are: Araneae (979 fossil species), Actinotrichida (283), Eurypterida (241), Scorpiones (111), Xiphosura (96), Trigonotarbida (71), Pseudoscorpiones (38), Phalangiotarbida (30), Opiliones (25), Ricinulei (15), and Anactinotrichida (11). Other groups are represented by ten fossil species or fewer. Based on published descriptions, spiders thus appear to dominate the fossil arachnid species assemblage, making up a greater proportion of paleodiversity than their Recent diversity would predict. Scorpions are also overrepresented, particularly in the Paleozoic, compared to their modern diversity. By contrast, groups like mites, harvestmen, pseudoscorpions and solifuges are noticeably under-represented as fossils when compared to modern patterns of diversity.

Keywords: Chelicerata, Arachnida, diversity, fossil, species counts

Harvey (2002: table 1) reported a total – to December 2000 – of 97,682 valid species of Recent Arachnida; with the caveat that many more probably remain to be described. But how many species of fossil arachnids are there? Older figures of 366 valid fossil arachnid species names can be culled from Scudder (1891) and, some sixty years later, Petrunkevitch (1955: 48) had cataloged 505. Since that time there have been important developments in our understanding of arachnid paleontology (see, e.g., Selden 1993). New localities continue to yield new species, while amber spiders (e.g., Wunderlich 2004) have proved to be the major source of new names in recent years. That said, revision of historical types usually lowers diversity once synonyms or erroneously assigned fossils have been recognized. Here, we offer a modern summary of crude fossil arachnid diversity (Table 1) and the most important localities (Table 2) as a baseline for future paleoarachnological research. 1593 valid fossil arachnid species are recognized here from 1776 published names. For completeness we have expanded our review to cover the entire Chelicerata, resulting in a grand total of 1952 valid fossil species from 2283 published names.

METHODS

No single modern catalog of fossil arachnids and their relatives exists, thus data had to be compiled from various sources as outlined for each group below. Where available, we drew on existing catalogs and/or summary papers, plus additions to the fauna since these publications. Data were cross-referenced to the primary literature wherever possible. Also valuable were lists on Joel Hallan's website <http://insects.tamu.edu/research/collection/hallan/>. Here, we restrict counts of valid species to published names and revisions only; i.e., excluding thesis work or papers in progress. The total number of described names incorporates synonyms, *nomina dubia*, *nomina nuda*, and incorrectly assigned material. For some groups – spiders, mites and the extinct orders in particular – species numbers had to be largely compiled from the primary literature and, due to space limitations, not all sources could be included here in the citations. We eventually hope to produce a more detailed list including taxa, authors, localities, type repositories and references, either as a printed catalog or internet resource. In the meantime the authors are happy to make our provisional lists available on a "fair use" basis upon request.

RESULTS

Pycnogonida.—Nine fossil sea spiders have been described (Poschmann & Dunlop 2006; Charbonnier et al. 2007): one late Cambrian larva from the "Orsten" of Sweden, a Silurian species from the Herefordshire Lagerstätte, UK, four from the early Devonian Hunsrück Slate of Germany and three from the Jurassic of France. Putative fossil sea spiders described from the Jurassic of Germany appear to be misidentified crustaceans.

"Euchelicerata".—An enigmatic Silurian fossil from the Herefordshire Lagerstätte, UK was described as having "chelicerate affinities" (Orr et al. 2000). Since it has opisthosomal opercula – a defining character of Euchelicerata – it can probably be assigned to this clade. Four further species are provisionally listed as "euchelicerates" in our database, but they are primarily there because they are poor fossils of indeterminate affinity.

Xiphosura.—Horseshoe crabs are unique among living chelicerates in that there are far more fossil species than the four living ones. That said, the temporal distribution of these species throughout their geological history suggests an overall

Table 1.—Valid fossil species of Chelicerata described to March 2008, divided into geological eras. See text for details of sources. Data includes subfossil (Quaternary: Holocene) occurrences of Recent species, of which 127 involve actinotrichid (oribatid) mites.

Group	Paleozoic	Mesozoic	Cenozoie	Total
Pycnogonida	6	3	—	9
"Euchelicerata"	5	—	—	5
Xiphosura	75	20	1	96
Chasmataspidida	8	—	—	8
Eurypterida	241	—	—	241
Scorpiones	79	16	16	111
Opiliones	7	1	17	25
Phalangiotarbida	30	—	—	30
Pseudoscorpiones	1	2	35	38
Solifugae	2	1	2	5
Acari: Anactinotrichida	—	1	10	11
Acari: Actinotrichida	15	15	253	283
Palpigradi	—	—	1	1
Ricinulei	15	—	—	15
"Pantetrapulmonata"	3	—	—	3
Trigonotarbida	71	—	—	71
Araneae	18	31	930	979
Haptopoda	1	—	—	1
Amblypygi	5	1	3	9
Uropygi	6	1	—	7
Schizomida	—	—	4	4
all Chelicerata	588	92	1272	1952
Arachnida only	253	69	1271	1593

diversity at any given time in the past similar to that seen today. In earlier studies various Paleozoic fossils vaguely resembling horseshoe crabs were assigned to Merostomata or even Xiphosura. Anderson & Selden (1997) excluded a number of these problematic taxa in their study of Paleozoic Xiphosura. These can be divided into a synziphosurine stem-lineage and a crown group Xiphosurida; the latter recently shown to extend back to the Ordovician (Rudkin et al. 2008). Data for Mesozoic and Cenozoic xiphosurids are mostly derived from Hauscke & Wilde (1991) and references therein. Currently, 96 xiphosuran species can be recognized, although revisions of Pennsylvanian genera (Anderson 1994, 1997) resulted in quite dramatic reductions in overall diversity. Most species-rich fossil genera appear to be over-split (Anderson 1996), with names based on preservational differences rather than convincing biological features. Further synonyms can be expected and the current total figure is probably an overestimate.

Chasmataspidida.—These little-known late Cambrian–mid Devonian marine euchelicerates are characterized by a long postabdomen of nine segments, but share prosomal features with both eurypterids and xiphosurans, rendering their monophyly and affinities uncertain. Seven chasmataspids were listed by Tetlie & Braddy (2004:table 1) and another was added by Poschmann et al. (2005). Both papers include further references and discussions of their morphology and relationships.

Eurypterida.—The extinct eurypterids, or sea scorpions, are the most diverse Paleozoic chelicerates. They ranged from the Ordovician to the Permian, with a clear peak of diversity in the Silurian. Tetlie (2007) provided a recent overview of their distribution and phylogeny. Tollerton (2004) proposed that some 29 Ordovician species are pseudofossils; i.e., sedimentary structures that fortuitously resemble animal material. Excluding these, our provisional list – drawing largely on Tetlie (2004) – documents 241 currently valid eurypterid species names. However, previous workers had a habit of assigning poor-quality specimens to common genera and Tetlie's study suggests that about fifty of these names are potentially synonyms, or otherwise based on non-diagnostic material. Thus, a final figure of c. 190 species may prove more realistic. Further revisions are needed, especially among the families Pterygotidae – which includes the largest recorded arthropods – and Adelophthalmidae, which are common in Coal Measures environments.

Scorpiones.—Whereas the fossil record of most (extant) arachnid orders is skewed towards the Cenozoic by large numbers of amber species, the scorpion fossil record is uniquely more diverse in the Paleozoic (Table 1). Drawing on the comprehensive posthumous monograph of Kjellesvig-Waering (1986), Fet et al. (2000) recognized 97 valid fossil scorpion species. Scorpions are the only arachnid order with a well-defined (Paleozoic) stem- and crown-group fossil record. A major question is whether the large number of Mississippian–Pennsylvanian taxa reflects a genuine period of radiation and experimentation – at least three major lineages appear to co-occur during this time – or to what extent this is an artifact of fossil abundance. Kjellesvig-Waering's monograph is problematic in that many Paleozoic specimens were not merely described as new species, but assigned their own family and/or superfamily group. A recent revision by Dunlop et al. (2008) synonymized two Silurian species, and with them eight superfluous higher taxa. Compared to their Paleozoic record, Mesozoic and Tertiary scorpions are quite rare. However, recent work has recovered increasing numbers from amber (Santiago-Blay et al. 2004; Lourenço & Weitschat 2005; and references therein), yielding a current total for all fossil scorpions of 111 valid species.

Opiliones.—The harvestman fossil record was reviewed by Dunlop (2007) who recognized 25 valid species and discussed the status of a number of fossils erroneously assigned to this group. The oldest harvestman is a eupnoid from the Rhynie chert and this is followed by a handful of Mississippian and Pennsylvanian species from Europe and North America. A single named Mesozoic example is known from Myanmar (Burmese) amber. The largest species assemblages come from Cenozoic ambers and the Florissant in Colorado, USA. Representatives of all four major lineages (or suborders) have now been found. The putative Pennsylvanian arachnid order Kustarachnida – with effectively only one valid species – is a misidentified harvestman and has thus been included in the Opiliones data. Descriptions of new species from amber are currently in preparation.

Phalangiotarbida.—This extinct order ranges from the Early Devonian to the Early Permian and is most common in the Coal Measures of Europe and North America. Petrunkevitch (1953) listed 24 species, plus one dubious taxon (excluded from Table 1); all under the order name Architarbi. There has been no formal revision of this species assemblage, but at least one (lost) fossil managed to get itself named three times which is fairly indicative of the quality of work thus far; see Rößler et al. (2003) for details. A posthumous Kjellesvig-Waering

Table 2.—Significant localities yielding fossil Chelicerata referred to in the text, including details of their stratigraphic position and approximate age in millions of years (Ma). Ages based primarily on the geological time chart of the British Geological Survey <http://www.bgs.ac.uk/education/britstrat/home.html>.

Locality	Country	Period	Epoch	Ma
Onyx Marble, Arizona	USA	Neogene	Pliocene?	2–5?
Dominican amber	Dominican Republic	Neogene	Miocene	16
Chiapas (Mexican) amber	Mexico	Neogene	Miocene	16
Randecker Maar	Germany	Neogene	Miocene	17
Aix-en-Provence	France	Palaeogene	Oligocene?	22?
Florissant, Colorado	USA	Palaeogene	Eocene	34
Baltic amber	Baltic coast of Europe	Palaeogene	Eocene	44–49
Canadian amber	Canada	late Cretaceous	Campanian	c. 78
Sierra de Montsech	Spain	late Cretaceous	Santonian	84
New Jersey amber	USA	late Cretaceous	Turorian	90–94
Myanmar (Burmese) amber	Myanmar	late Cretaceous	Albian	c. 100
Crato Formation	Brazil	early Cretaceous	Aptian	115
Álava amber	Spain	early Cretaceous	Aptian	115–121
Lebanese amber	Lebanon	early Cretaceous	Nec.–Aptian	130
Coal Measures	Europe / N. America	Pennsylvanian	Nam.–Steph.	327–290
Gilboa, New York State	USA	mid Devonian	Givetian	380
Hunsrück Slate	Germany	early Devonian	Emsian	390
Rhynie Chert, Scotland	UK	early Devonian	Pragian	410
Herefordshire Lagerstätte	UK	Silurian	Wenlock	425
"Orsten"	Sweden	late Cambrian	—	c. 500

manuscript mentioned in Selden (1993) proposed a number of synonymies, but was never formally published. Since Petrunkevitch's monographs a few new descriptions have been published, including the oldest record (Poschmann et al. 2005), such that 30 valid species can currently be recognized.

Pseudoscorpiones.—Harvey (1991) listed 32 valid fossil pseudoscorpions derived from Myanmar, Chinese, Baltic, and Dominican amber (see also Spahr 1993:12–20). Two further species were treated as *nomina dubia* by Harvey. Also not included as a valid species here is a questionable assignment, listed in Spahr, of a fossil in Romanian amber with affinities to an extant species. Since Harvey's catalogue, we can add the oldest record of the group from the mid Devonian of Gilboa, New York State (Schawaller et al. 1991). This, and further amber records (e.g., Henderickx 2005; Judson 2007), yield a current total count of 38 valid fossil species.

Solifugae.—Five fossil camel spider species are known, including a putative stem-group species from the Mississippian of Poland, a poorly-preserved example from the Coal Measures of Mazon Creek, Illinois, USA, one from the Cretaceous Crato Formation of Brazil, and two in Baltic and Dominican amber respectively; see Dunlop et al. (2004) for further details and literature.

Anactinotrichida.—Fossil anactinotrichid mites (Parasitiformes in some terminologies) are surprisingly rare given their modern diversity – eleven fossil species in total – and currently have a record no older than the late Cretaceous. They include an opilioacarid from Baltic amber (Dunlop et al. 2004), five named gamasid (or mesostigmatic) species from Baltic and Mexican amber (e.g., Witlański 2000), and five ticks (reviewed by Fuente 2003), mostly from various Mesozoic and Tertiary ambers.

Actinotrichida.—Actinotrichid mites (Acariformes in some terminologies) have a much more diverse, and a much older, fossil record. A putative Ordovician oribatid was not formally named, thus the oldest described actinotrichids come from the Rhynie chert of Scotland and from Gilboa, New York, USA (both Devonian). Further Devonian and Mississippian mites have been recovered from macerates (Subías & Arillo 2002), after which there is a considerable hiatus in the fossil record until mites begin to be formally described again in the mid Mesozoic. Amber is a major source of taxa and Spahr (1993) listed 129 actinotrichids across all ambers. A few amber species have been described since (e.g., Judson & Wunderlich 2003; Norton 2006), while various non-amber sources, like Aix-en-Provence in France (Gourret 1887), contribute to the fossil record too. Taxonomically, the best represented group are oribatids; presumably thanks to their often strongly sclerotized bodies. Their fossil record was reviewed by Krivolutsky & Druck (1986), and Norton (2006) partially revised the Baltic amber species. It is also worth noting that there is an extensive record of subfossil (Holocene) oribatid mites (e.g., Karpinen et al. 1979) from ancient soils and peats only hundreds or thousands of years old. All can be assigned convincingly to Recent species and comprise 127 of the fossil names in our data. Whether they should truly be considered fossils is a moot point, but we have included them in our calculations for completeness. Together with the other (extinct) species this gives a total fossil record of 283 actinotrichid names. Frequent reports of unnamed mites, particularly from various Mesozoic ambers, suggest that this number is a serious underestimate.

Palpigradi.—A single, ?Pliocene, fossil palpigrade has been described from the Onyx Marble of Arizona, USA (Rowland & Sissom 1980). A putative record from the Jurassic of Germany is a misidentified insect; see also Harvey (2002).

Ricinulei.—Fossil ricinuleids were revised by Selden (1992). All originate from the Pennsylvanian Coal Measures of Europe and North America. Fifteen valid fossil species in

four genera and two families were recognized and no new taxa have been described since.

"Pantetrapulmonata".—Three Devonian arachnid species could not be assigned to any specific order, but were listed – partly for convenience – as probable members of this clade (Dunlop et al. 2006).

Trigonotarbida.—This extinct order ranges from the late Silurian to the early Permian and is most common in the Pennsylvanian Coal Measures of Europe and North America. Petrunkevitch (1953) listed 52 valid species – combining data for Trigonotarbida and its synonym Anthracomartida – plus five dubious taxa; at least one of which has since been revalidated (Dunlop & Rössler 2002). There has been considerable movement since Petrunkevitch's monographs, both in terms of revising older taxa and describing new ones. More remains to be done, especially among the common and clearly over-split Anthracomartidae (see comments in Dunlop & Rössler 2002), but our dataset recognizes 71 currently valid species names.

Araneae.—Penney & Selden (2007) provided a brief, general review of the spider fossil record. The oldest example comes from the Devonian of Gilboa, New York, USA (Selden et al. 1991) and a number of Pennsylvanian mesothele-like taxa have been recorded, the affinities of which are currently being revised (P. Selden, pers. comm.). The oldest unequivocal mesothele is late Pennsylvanian and both mygalomorphs and araneomorphs have now been recorded from sedimentary deposits in the Triassic. The vast majority of fossil spiders, c. 820 species, originate from amber. Around 540 species have been recorded from Eocene Baltic amber alone and Wunderlich (2004:203) speculated that three times this number may eventually be recovered from this one deposit. Miocene Dominican amber ranks second with approximately 170 named species (Penney 2006a) and the geographically and stratigraphically contemporary Chiapas (Mexican) amber yields about twenty (e.g., Petrunkevitch 1971). Other Cenozoic ambers – e.g., Parisian (France), Bitterfeld (Germany), Rovno (Ukraine) and China – are beginning to yield spiders too, as are various younger resins or copals; see studies in Wunderlich (2004). Significantly, an increasing number of species have been described in recent years from Cretaceous ambers such as Taimyr, Siberia (Eskov & Wunderlich 1995), Manitoba, Canada, Myanmar (= Burma) (Penney 2006b), New Jersey (Penney 2004a), the Isle of Wight, UK (Selden 2002); Álava (Spain) (Penney & Ortuño 2006) and Lebanese amber (Penney 2003).

Non-amber fossil spiders are much less common, but also derive from a wide range of localities. In addition to the Coal Measures, the most species-rich of these include the Cretaceous of Mongolia and Siberia (Eskov & Zonshtein 1990), Sierra de Montsech, Spain (Selden & Penney 2003), and the Brazilian Crato Formation (Selden et al. 2006). Also significant are the Cenozoic localities of Aix-en-Provence, France (Gourret 1887; Berland 1939), Florissant, Colorado, USA (Petrunkevitch 1922), Shanwang, Shandong, China (Zhang et al. 1994) and the Randecker Maar, Germany (Schawaller & Ono, 1979). Subfossil spiders from peat bogs can also be identified and assigned to extant species (Scott 2003) and these records have been included in our lists. Our total dataset for amber and non-amber spiders yields 979 fossil species; thus spiders show the highest levels of paleodiversity – approaching three times as many species as the next largest chelicerate groups (Table 1).

Haptopoda.—This extinct, monotypic, Coal Measures order was restudied by Dunlop (1999). Its status as a distinct order was confirmed, but no further species have been assigned to it.

Amblypygi.—Six species of fossil whip spider are listed in Harvey (2003:22, 30–32), four from the Coal Measures of Europe and North America and two in extant families from Mexican and Dominican amber respectively. Following Harvey, a dubious record from Aix-en-Provence (Gourret 1887) has been excluded. An overlooked Coal Measures name, a new species from the Crato Formation of Brazil (Dunlop & Martill 2002), and one from Mexican amber (Poinar & Brown 2004) bring the total number of currently valid species to nine.

Uropygi.—Nine species of fossil whip scorpion are listed by Harvey (2003:73–74, 79–80); and one further Pennsylvanian species was overlooked. Tetlie & Dunlop (2008) recognized only six species from the Coal Measures of Europe and North America (one of which may actually be a stem-group schizomid). There is a further species from the Crato Formation of Brazil (Dunlop & Martill 2002), yielding a current total of seven, but a putative species from the Miocene of California, USA is a misidentification.

Schizomida.—Four Tertiary species of fossil schizomid in three genera have been described. Three come from the Onyx Marble of Arizona, USA and one from the Oligocene of China. Further details can be found in Harvey (2003:103, 129). No further species have since been recorded, although schizomids from Dominican Republic amber will be described shortly.

DISCUSSION

Comparing measures of fossil (Table 1) and Recent (Harvey 2002) biodiversity, our species counts imply that the arachnid fossil record is biased in favor of spiders and scorpions. These two orders make up a greater percentage of total fossil diversity compared to their relative abundance in modern ecosystems today. Correspondingly, the fossil record is biased against mites, harvestmen, pseudoscorpions and solifuges. Mites make up almost half of all living arachnid species, but less than a fifth of the fossil paleodiversity. Part of the explanation must be the greater intensity of work on fossil spiders (cf. Wunderlich 2004 and references therein) and to a lesser extent scorpions (Kjellesvig-Waering 1986). By contrast we recognize a corresponding lack of effort, or expertise, when it comes to members of the Acari, Opiliones, Pseudoseorpiones, and the "minor" orders. Physically small taxa, like mites and pseudoscorpions, are generally less likely to be preserved (or noticed). Solifuges tend to be associated today with dry habitats and conditions for fossilization are most favorable where there are substantial bodies of water into which animals can fall and be buried.

It is important to stress that these crude species counts encompass the entire fossil record and to caution against over-interpreting data combined from different time periods and under different conditions of fossilization. Arachnids, and other chelicerates, lack a mineralized exoskeleton, thus their fossil record is sporadic and relies heavily on "windows" of exceptional preservation (Table 2). This makes it difficult to

trace changes in their biodiversity over geological time with any accuracy, since apparent peaks of species-level diversity in the raw data largely reflect productive fossil localities like the Coal Measures or intensively investigated ambers. Nevertheless, superimposing the fossil record onto well-supported cladograms allows the construction of "evolutionary trees." Since a given taxon must be as old as its sister-group (which may not be preserved) these trees have considerable value in predicting which lineages should have been present during any given time period. They allow quantitative studies of faunal change, such as Penney et al.'s (2003) demonstration that spider families were not affected by the K-T mass extinction event, or Penney's (2004b) use of richness estimates to show how spider radiations seem to track the radiation of their insect prey over geological time. It is our hope that the raw data we are assembling here can allow similar quantitative studies to be expanded and applied to Chelicerata as a whole.

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Intercontinental Triaenonychidae—the case of *Ceratomontia* (Opiliones, Insidiatores)

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Abstract. Among the 64 genera of Triaenonychinae Sorensen 1886 (Opiliones, Insidiatores), two are found in more than one continent: *Ceratomontia* Roewer 1915 and *Nuncia* Loman 1902, both occurring in South America, the former occurring also in South Africa, the latter in New Zealand. Until now there were 22 valid species of *Ceratomontia*, diagnosed mainly by the tarsal formula. In the present paper, a cladistic analysis was performed to test the monophyly of *Ceratomontia* and study its relationship with the South African triaenonychine genera *Austromontia* Lawrence 1931 and *Monomontia* Lawrence 1931. A total of 42 morphological characters were coded for 18 terminal taxa, 14 representing the genera *Ceratomontia* (from South America and South Africa), *Austromontia* and *Monomontia* as ingroup, and two species of Triaenonyehinae from South Ameriea, one from South Africa and one Adaeinae Pocock 1902 from South Africa as outgroups. The analysis using heuristic search algorithms resulted in 12 most parsimonious trees (L = 95, CI = 0.52, RI = 0.66). The consensus hypothesis did not recover a monophyletic *Ceratomontia*, instead, the South African species constitute a clade with the *Austromontia* and *Monomontia* species. The *Ceratomontia* species from South America form a clade that is sister-group of the clade formed by the South African genera of the ingroup. The result shows that *Ceratomontia* is involved in a "Gondwanan relationship," but also includes other genera, suggesting that it is not a monophyletic group.

Keywords: Temperate Gondwana, South Africa, South America, Laniatores, cladisties

The harvestman family Triaenonychidae Sørensen 1886 (Opiliones) includes about 480 described speeies (Kury 2003). It is the third most diverse family of the suborder Laniatores Thorell 1876 and the most diverse of the infra-order Insidiatores Loman 1902 (sensu Kury 2003). It includes small-sized Laniatores and is characterized by the single claws of legs III–IV bearing at least one pair of lateral prongs. The family is mainly distributed in the former Temperate Gondwana, constituting the dominant opilionofauna in New Zealand, Madagascar, and South Africa, also occurring in Australia and southern South America. It also includes representatives in the Northern Hemisphere as the subfamilies Sclerobuninae Dumitrescu 1976, Paranonychinae Briggs 1971, both Nearctic – the latter also occurring in Japan, Kaolinonychinae Suzuki 1976 and Nippononyehinae Suzuki 1976 both from Eastern Asia (Japan and Korea), and the species *Fumontana deprehendor* Shear 1977 currently assigned as a member of Triaenonychinae, from the eastern United States (Shear 1977, 1978; Thomas & Hedin 2006). Although the allocation of those subfamilies endemic to the Holarctic region into Triaenonychidae has been recently challenged (Giribet & Kury 2007); there is not yet any detailed study on this matter.

Among the 64 genera of Triaenonychinae Sørensen 1886, two have been reported to occur in more than one continent: *Ceratomontia* Roewer 1915 and *Nuncia* Loman 1902, both occurring in South America, the former oceurring also in South Africa, the latter also in New Zealand. There are currently 22 valid species of *Ceratomontia*: 18 in South Africa, including the type species *C. capensis* Roewer 1915, and four occurring in Argentina, Uruguay and south of Brazil.

The genus, as with most genera described by the German arachnologist Carl Friedrich Roewer (e.g., Roewer 1915, 1923), is mainly diagnosed by the tarsal formula of the type species (= 2-3-3-3). Lawrence (1931, 1934, 1937) emended Roewer's diagnosis (Roewer 1915) with some characters of the pedipalpus and described an additional 17 species in the genus from South Africa; one (*C. hewitti* Lawrence 1931) later synonymized by Staręga (1992). Canals (1939) described the first South American species for the genus, *C. argentina* Canals 1939, justifying the generic allocation by the presence of all the characters assigned to *Ceratomontia* by Roewer (1915) and almost all the characters aggregated by Lawrence (1931) except for the number of tubercles in the anterior margin of the ventral surface of coxa I. Two other South American species were described in the genus by Maury & Roig-Alsina (1985) and another by Maury (1999), also based mainly on the tarsal formula. Kauri (1961) divided the South African genera of Triaenonychinae into two groups: the *Ceratomontia* group, including 11 genera with a longitudinal band of fine granulation on the ventral surface of the pedipalpal femur, and the *Roeweratia* group, including nine genera without the band. Kauri (1961) also noted the resemblance of the male genitalia between the genera *Ceratomontia*, *Austromontia* Lawrence 1931, and *Monomontia* Lawrence 1931 (Kauri 1961: 75) but the basic character used to identify the genera that are included in his key (since he did not provide diagnoses), is the tarsal counts.

This work aims to test the monophyly of *Ceratomontia* as an intercontinental genus and verify the relationship between it and two of the genera included in the *Ceratomontia* group *sensu* Kauri, *Austromontia* and *Monomontia*, given the resemblance of external morphology and genitalia among those taxa.

METHODS

The specimens studied herein are deposited in the following collections: American Museum of Natural History, New York (AMNH), Museu Nacional/Universidade Federal do Rio de Janeiro (MNRJ), Collection Helia Eller Monteiro Soares, formerly a private collection, today on behalf of MNRJ

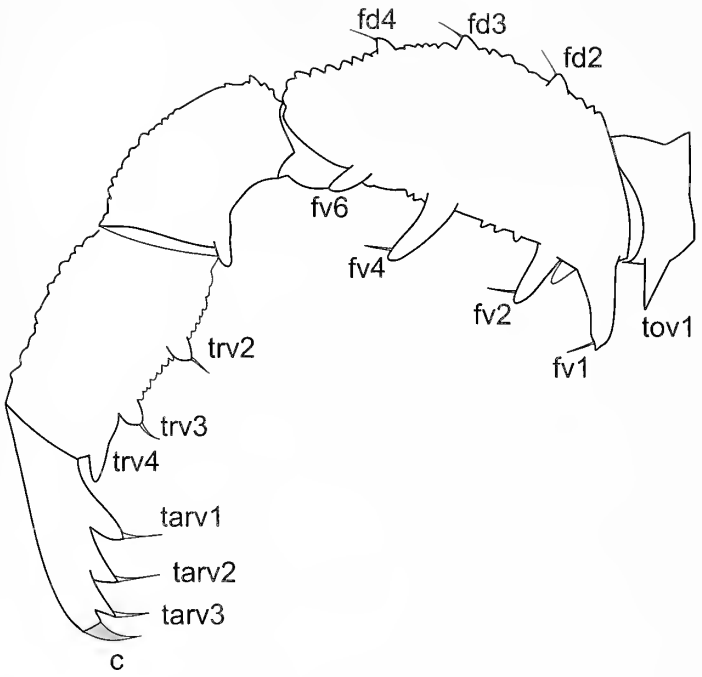

Figure 1.—*Larifuga capensis*. Retrolateral view of left pedipalpus. Setae terminology based on Hunt & Hickman (1993:82, fig. 1); tov = trochanter ventral; fd = femur dorsal; fv = femur ventral; tarv = tarsus retroventral; c = claw.

(HEMS), National Collection of Arachnida, Pretoria (NCA), Transvaal Museum, Pretoria (TM). The specimens were examined using a Wild Heerbrugg M8 stereomicroscope fitted with a camera lucida for drawings. Male genitalia were dissected and temporarily mounted on microscope slides with 1 cm coverslips supported by two slivers of broken coverslips, with two-three droplets of glycerol. They were observed using a Nikon E-200 compound microscope and after study returned to 75% ethanol in microvials kept with their respective specimen.

For pedipalpal setae we used the terminology created for Triaenonychidae by Hunt & Hickman (1993), specified here in Fig. 1. For male genitalia we used Martenss (1986) terminology adapted by Hunt & Hickman (1993). The figures of the present paper are referred to with a capital letter (i.e., "Fig."); figures of other papers are referred in lower case (i.e., "fig.").

Cladistic Analysis.—The ingroup consists of the type species of *Ceratomontia* and two other species occurring in South Africa as well as all four species occurring in South America (Argentina, south of Brazil, and Uruguay), besides three species of *Austromontia* and four of *Monomontia*. The outgroup is composed of two genera of South American Triaenonychinae, one of the South African Triaenonychinae and one representative of a South African genus of Adaeinae Pocock 1902. Table 1 provides the list of species used as terminals in the analysis, indicating their distribution and source of information used.

A total of 42 morphological characters were coded for 18 terminal taxa. The characters were treated as unordered and the polarization was made *a posteriori*, resulting from the rooting of the diagrams obtained by the parsimony analysis (Nixon & Carpenter 1993). The coding for the terminals is shown in Table 2. An analysis using heuristic search algorithms with random addition-sequence (1000 replicates) and with equal weights and tree-bisection-reconnection (TBR) branch swapping was performed using the program NONA version 2.0 (Goloboff 1993c). Branch-support was evaluated through Bremer support (Bremer 1994) and bootstrap (Felsenstein 1985), both performed using NONA, via WinClada (Nixon 2002) in the case of bootstrap analysis, which was made with 2000 replicates with TBR swapping. We studied the distribution and optimization of the characters also through the program WinClada.

We also performed an analysis under implied weights using the program PIWE version 3.0 (Goloboff 1993a, b). As long as there is not a consensus in the literature in respect to the adequate value of the concavity constant k (e.g., Turner & Zandee 1995), we conducted the analyses with k = 1–6 to observe the effect of the constant variation over the topology of the trees. The evaluation of stability of results through different parameters, such as different concavity values (k), is comparable to a sensitivity analysis (Wheeler 1995) used in molecular analyses. This was done before by other authors in phylogenies using morphological data (Prendini 2003; de Bivort & Giribet 2004). The analyses using implied weighting were also performed using heuristic search algorithms and TBR branch swapping.

CLADISTIC ANALYSIS

Characters.—The characters used in the analysis are listed below.

Dorsal structures

1. *Anterior margin, ornamentation of tubercles*, **(0)** absent; **(1)** present (Maury & Roig-Alsina 1985:fig.18).
2. *Anterior margin, number of tubercles*, **(0)** two; **(1)** three; **(2)** four; **(3)** five.
3. *Eyemound, length in relation to the width*, **(0)** much larger, at least twice as large (Fig. 2A, B; Maury & Roig-Alsina 1985:fig. 17); **(1)** less than twice as large (Fig. 2C; Maury & Roig-Alsina 1985: fig. 19).
4. *Eyemound, median spine aspect*, **(0)** continuous with the eyemound (conic aspect) (Fig. 2A); **(1)** independent of the eyemound base (Fig. 2B).
5. *Eyemound, direction*, **(0)** upwards (dorsally pointed) (Fig. 2B); **(1)** slightly anteriorly directed; **(2)** conspicuously anteriorly directed (Fig. 2A)
6. *Eyemound, groove between eyemound and the posterior region of the carapace*, **(0)** absent; **(1)** present (Kauri 1962:fig. 49A).
7. *Mesotergal areas, definition*, **(0)** poorly defined (shallow); **(1)** well defined (deep).
8. *Mesotergal areas I–IV, pair of tubercles*, **(0)** present; **(1)** absent.
9. *Posterior margin and free tergites, kind of ornamentation*, **(0)** row of conspicuous conical tubercles or apophyses; **(1)** row of small granules.

Appendages

10. *Chelicera, basichelicerite, bulla*, **(0)** weakly defined; **(1)** conspicuous (rounded).
11. *Chelicera, basichelicerite, dorsal distal margin, setalspine*, **(0)** absent; **(1)** present.

Table 1.—List of species (outgroup and ingroup) used in the present cladistic analysis with distribution and source of information used (literature or material).

Subfamily	Species	Distribution	Source of information used
Adaeinae	*Larifuga capensis* Lawrence 1931	S. Africa	MNRJ18809
Triaenonychinae (outgroup)	*Gunvoria spatulata* Kauri 1961	S. Africa	MNRJ18807
	Naluelonyx nasutus (Ringuelet 1959)	Argentina	AMNH (no catalog number)
	Nuncia spinulosa Maury 1990	Argentina	AMNH (no catalog number)
Triaenonychinae (ingroup)	*Austromontia bidentata* Lawrence 1934	S. Africa	Kauri 1961
	A. capensis Lawrence 1931	S. Africa	TM15586, TM15597
	A. silvatica Lawrence 1931	S. Africa	AMNH (no catalog number)
	Ceratomontia argentina Canals 1939	Argentina	Maury & Roig-Alsina 1985
	C. brasiliana Maury 1999	Brazil	HEMS706
	C. capensis Roewer 1915	S. Africa	NCA 81/501
	C. centralis Maury & Roig-Alsina 1985	Argentina	Maury & Roig-Alsina 1985
	C. mendocina Maury & Roig-Alsina 1985	Argentina	Maury & Roig-Alsina 1985
	C. minor Lawrence 1931	S. Africa	Kauri 1961
	C. tabulae Lawrence 1931	S. Africa	Kauri 1961
	Monomontia brincki Kauri 1961	S. Africa	Kauri 1961
	M. corticola Lawrence 1938	S. Africa	Kauri 1961
	M. lawrencei Kauri 1950	S. Africa	Kauri 1961
	M. rugosa Lawrence 1937	S. Africa	TM15368

12. *Pedipalpal femur, dorsal surface ornamentation*, **(0)** present (Kauri 1961:fig. 45C); **(1)** absent.
13. *Pedipalpal femur, dorsal surface, kind of ornamentation*, **(0)** row of setae; **(1)** row of flattened tubercles.
14. *Pedipalpal femur, dorsal surface, structure and distribution of setae*, **(0)** fd2, fd3 and fd4 reaching almost the apex (Fig. 1); **(1)** fd2, fd3, and fd4 reaching half of the femur; **(2)** fd1–fd5 from basis to the apex.
15. *Pedipalpal femur, setae fv3–fv6*, **(0)** all absent; **(1)** present (at least fv4 and fv6) (Fig. 1).
16. *Pedipalpal femur, fv1, length in relation to the other fvs*, **(0)** larger; **(1)** same size.
17. *Pedipalpal femur, fv1 aspect*, **(0)** bifid (Lawrence 1931:fig.15d); **(1)** uniramous (Maury & Roig-Alsina 1985:figs. 9, 11).
18. *Pedipalpal femur, ventral surface, band of small granules*, **(0)** absent; **(1)** present (Kauri 1961:fig. 49C).
19. *Pedipalpal femur, fpl2*, **(0)** absent; **(1)** present (Lawrence 1931:fig.12C).
20. *Pedipalpal femur, shape of the basis of ventral setae*, **(0)** conical (Kauri 1961:fig. 49B); **(1)** cruciform (Maury & Roig-Alsina 1985:figs. 1, 3, 5, 7).
21. *Pedipalpal tibia, size in relation to the femur*, **(0)** incrassate, comparable size; **(1)** not incrassate, much smaller.

Table 2.—Character and character state data matrix for selected members of the genera *Ceratomontia*, *Austromontia* and *Monomontia* and outgroup taxa. '-' code for inapplicable, '?' for unavailable, and 'a' for the polymorphism 0+1.

	1																				**2**																**3**										**4**		
Terminal taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**
Larifuga capensis	1	3	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	1	0	1	-	0	2	0	1	0	1	0	0	1	1	0	2	1	0	1	0
Gunvoria spatulata	0	-	0	1	1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	-	0	0	0	0	?	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0
Naluelonyx nasutus	1	1	0	1	2	0	0	0	0	?	1	1	-	-	0	-	-	0	0	-	1	-	0	0	0	1	-	1	0	1	0	1	1	1	1	1	0	2	0	0	0	0
Nuncia spinulosa	0	-	0	1	?	0	?	?	?	0	0	0	0	0	2	1	0	0	0	0	0	1	?	1	0	0	?	1	2	0	1	0	0	-	0	1	1	0	2	1	2	0	0
Monomontia brincki	1	1	1	0	0	1	1	1	1	0	1	0	0	-	1	0	1	1	1	0	?	0	1	?	?	?	?	?	1	1	1	?	0	-	0	0	1	1	1	1	0	0	1
M. corticola	1	1	1	0	1	1	1	1	1	0	?	0	0	?	1	0	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	1	1	1	1	0	0	1
M. lawrencei	1	2	0	0	2	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	?	0	0	0	1	1	1	1	1	0	0	0	1	1	1	?	0	0	1
M. rugosa	1	2	0	0	2	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	?	0	0	0	1	1	1	1	1	0	0	0	1	1	1	?	0	0	1
Austromontia silvatica	0	-	1	0	0	1	1	1	1	1	1	0	0	1	?	1	1	1	0	0	0	0	1	1	0	1	0	1	1	1	1	1	1	0	1	?	?	?	0	0	1
A. bidentata	1	0	1	0	2	1	1	1	1	1	1	0	0	1	1	0	1	1	0	0	?	?	?	?	?	?	0	1	1	1	?	1	0	1	0	1	1	0	2	0	0	1
A. capensis	1	a	0	0	2	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	?	?	?	0	0	1
Ceratomontia argentina	1	3	0	0	2	?	1	0	1	0	?	0	0	2	1	1	1	?	0	1	1	?	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	2	-	1	1	1
C. brasiliana	0	-	1	-	2	0	1	0	1	1	1	0	0	2	1	1	1	1	0	1	1	-	0	0	?	?	?	0	1	0	1	1	1	0	0	0	1	2	-	1	1	1
C. capensis	1	0	0	0	2	1	1	1	1	1	1	0	0	1	0	0	1	1	1	0	1	1	0	0	0	0	?	0	1	0	1	1	0	0	0	1	1	1	1	0	0	1
C. centralis	1	2	0	0	2	?	1	0	1	0	?	0	0	2	1	1	1	?	0	1	1	?	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	2	-	1	1	1
C. mendocina	?	?	1	0	2	?	1	1	1	0	?	0	0	2	1	1	1	?	0	0	1	?	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	2	-	1	1	1
C. minor	1	0	1	0	0	1	1	1	1	?	?	0	0	0	0	0	0	1	1	0	?	0	1	0	0	0	0	0	1	0	?	1	0	0	0	1	1	1	0	0	0	1
C. tabulae	1	0	1	0	0	1	1	1	1	1	1	0	0	0	1	0	0	1	1	0	?	?	?	?	0	0	0	0	1	0	?	1	0	0	0	1	0	1	0	0	0	1

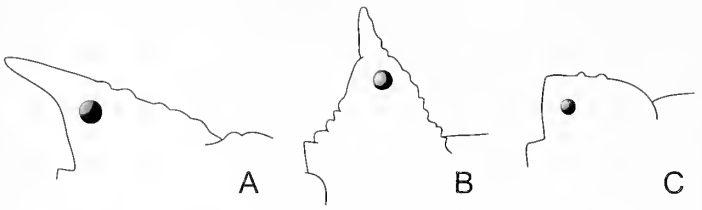

Figure 2.—Triaenonychinae eyemounds, lateral view. A. *Monomontia rugosa*. B. *Larifuga capensis*. C. *Austromontia silvatica*. Not to scale.

22. *Pedipalpal tibia, ventral surface, distribution of granules*, **(0)** organized into a mesal row (Lawrence 1931:fig.15b); **(1)** spread all over the ventral surface.
23. *Pedipalpal tibia and tarsus, spine sockets, size*, **(0)** small; **(1)** conspicuously large (Fig. 1).
24. *Pedipalpal tarsus, ectal margin, bifid projection*, **(0)** absent (Lawrence 1931:fig. 15b); **(1)** present (Lawrence 1931:figs. 29f, 30f).
25. *Coxa I, ventral surface aspect*, **(0)** tuberculate; **(1)** smooth.
26. *Coxa I, ventral surface, number of rows of tubercles*, **(0)** one; **(1)** two.
27. *Coxa I, tubercle on the distal margin, aspect of tip*, **(0)** conspicuously bifid (Fig. 3); **(1)** uniramous
28. *Tarsus I, number of tarsomeres*, **(0)** two; **(1)** three; **(2)** four.
29. *Tarsus II, number of tarsomeres*, **(0)** more than six; **(1)** less than six.
30. *Tarsus III and IV, number of tarsomeres*, **(0)** three; **(1)** four.
31. *Tarsus I, distal tarsomere, size in relation to the other tarsomere(s)*, **(0)** similar; **(1)** incrassate (Maury & Roig-Alsina 1985:figs. 2, 4, 6, 8).
32. *Femur I, ventral surface, tubercles organized into a row*, **(0)** absent; **(1)** present (Lawrence 1931:figs. 12b, 13d, 15d).
33. *Femur I, ventral surface, tubercles shape*, **(0)** elongate (Maury & Roig-Alsina 1985:figs. 2, 4, 6, 8); **(1)** flattened (granules).
34. *Metatarsus I–II, calcaneus, length in relation to the podomere length*, **(0)** less than half (Maury & Roig-Alsina 1985:figs. 2, 4, 6, 8); **(1)** about half.

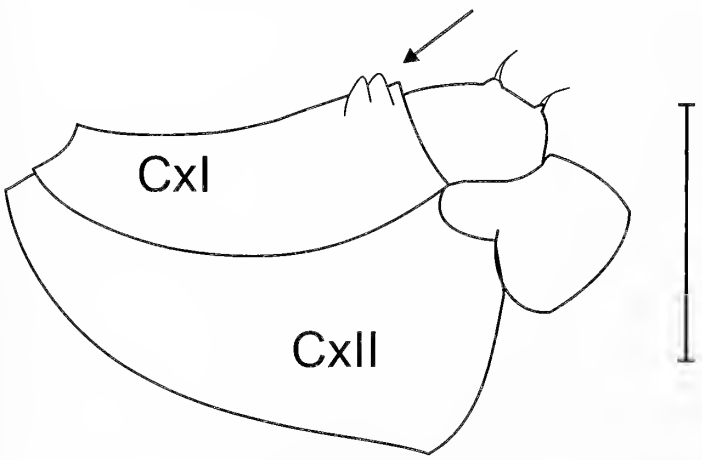

Figure 3.—*Austromontia silvatica*. Ventral view of the left coxa I–II. The seta points to the bifid tubercle on the distal margin of coxa I. Scale bar = 1 mm.

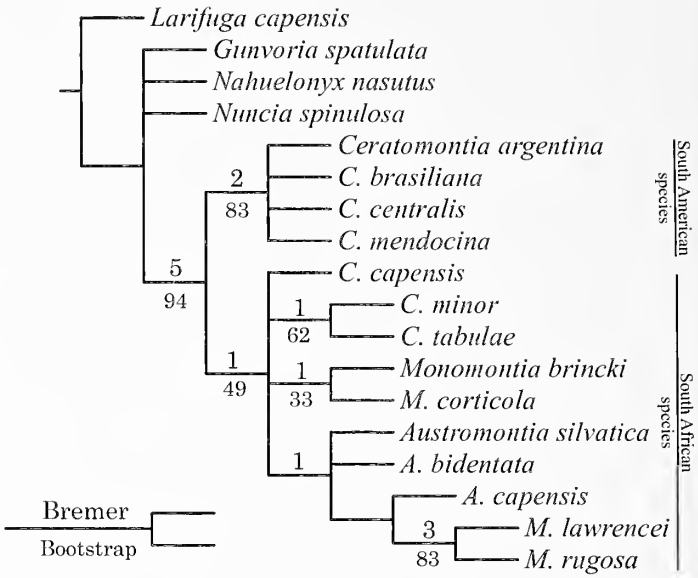

Figure 4.—Summary hypothesis of phylogeny of *Ceratomontia* and related genera *Austromontia* and *Monomontia*: strict consensus of the 12 most-parsimonious trees resulting from the analysis under equal weights at 95 steps (CI = 0.52, RI = 0.66). Clade support is indicated above (Bremer support) and below (bootstrap proportions) branches.

Male genitalia

35. *Dorsal plate, length in relation to the ventral plate*, **(0)** elongate, longer than the ventral plate (Maury & Roig-Alsina 1985:figs. 15, 16); **(1)** short, about same length or shorter than the ventral plate.
36. *Ventral plate, aspect (presence of a deep cleft)*, **(0)** entire (without any cleft) (Maury & Roig-Alsina 1985:fig. 16); **(1)** divided (with a deep cleft) (Kauri 1961:figs. 49F, 50A, 51A).
37. *Dorso-lateral plate, disto-ventral projections*, **(0)** absent; **(1)** present.
38. *Ventral plate, width of basis in relation to the apex*, **(0)** wider (Kauri 1961:fig. 54E); **(1)** narrower (Kauri 1961:figs. 45A, 46A, 49F, 50A, 51A); **(2)** same (Maury & Roig-Alsina 1985:fig. 16).
39. *Ventral plate halves, shape*, **(0)** rectangular (Kauri 1961:figs. 45A, 46A); **(1)** oval (rounded); **(2)** triangular (narrow apex) (Kauri 1961:fig. 54A).
40. *Sensilar region, number of setae*, **(0)** 4+4 (Kauri 1961:figs. 45A, 46A, 49F, 50A, 51A, 54A); **(1)** 5+5 (Maury & Roig-Alsina 1985:figs. 13–16); **(2)** 3+3.
41. *Sensilar region, setae distribution*, **(0)** all ahead (Kauri 1961:figs. 45A, 46A, 49F, 50A, 51A, 54A); **(1)** a part ahead and the other behind the ventral plate (Maury & Roig-Alsina 1985:figs. 13–16).
42. *Stylus position*, **(0)** independent; **(1)** enfolded by the dorsal plate (Maury & Roig-Alsina 1985, figs 15–16).

RESULTS

The analysis under equal weights resulted in 12 most parsimonious trees, with 95 steps, CI = 0.52, RI = 0.66. The strict consensus hypothesis (Fig. 4) does not recover a monophyletic *Ceratomontia*; instead, the South African species form a clade with the *Austromontia* and *Monomontia*

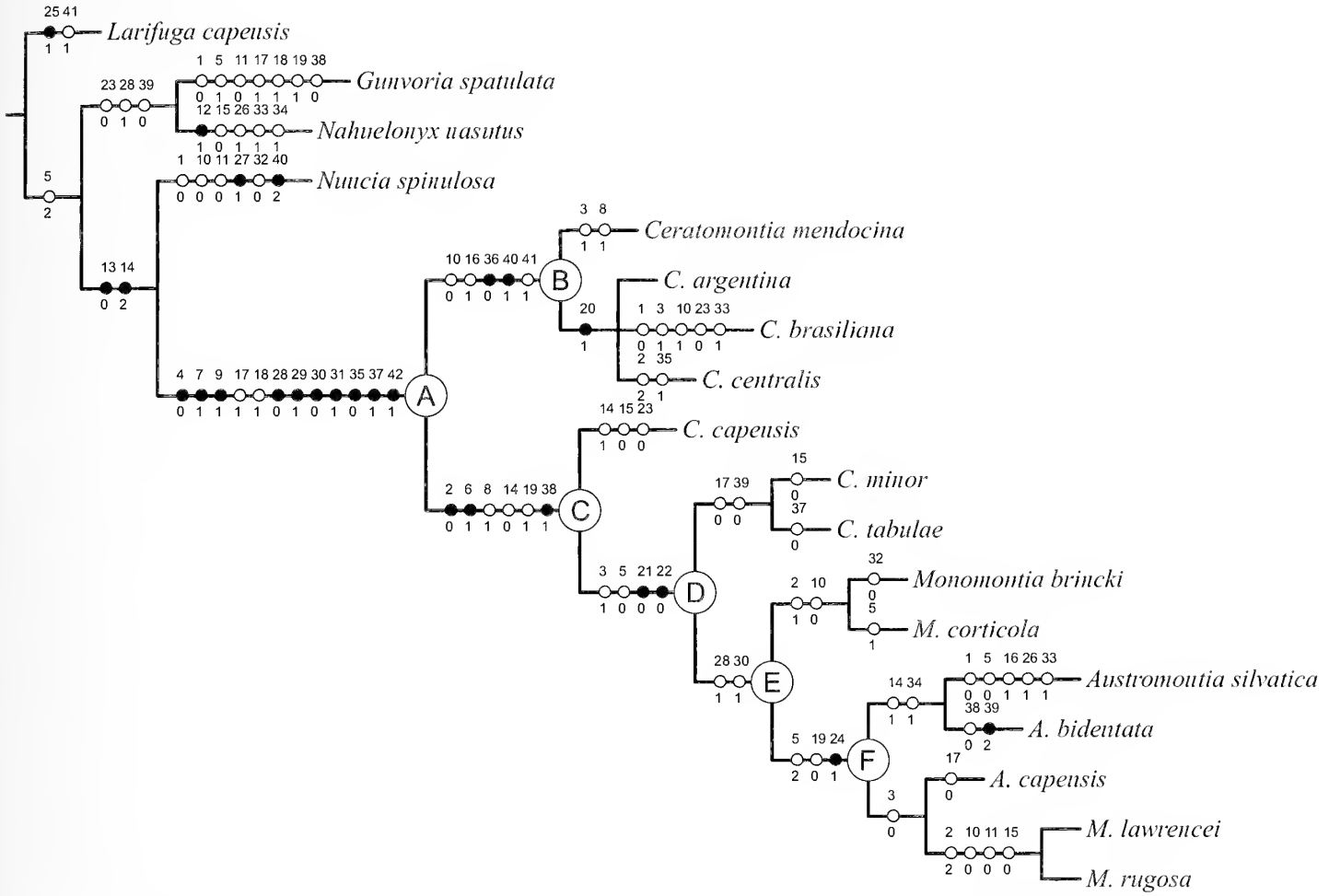

Figure 5.—Preferred hypothesis of phylogeny of *Ceratomontia* and related genera *Austromontia* and *Monomontia*: tree obtained from the analyses under implied weights with all concavities (k = 1–6) and one of the most parsimonious trees obtained from the analysis under equal weights. Apomorphies are plotted on branches, black circles indicate non-homoplastic apomorphies, empty circles indicate homoplastic apomorphies and reversals. (See Table 3 for details.) Certain nodes are named with letters (A–F) for usage in the text.

Table 3.—Apomorphy list for the preferred tree (Fig. 5) of the cladistic analysis of the genera *Ceratomontia*, *Austromontia*, and *Monomontia*. The names of the nodes follow Fig. 5. Non-homoplastic synapomorphies are in bold type, A codes ACCTRAN optimization, D codes DELTRAN optimization, and R reversion.

Node	Apomorphies
(*Gunvoria* + *Nahuelonyx*)	23(0); 28(1); 39(0)
(*Nuncia* + A)	**13(0); 14(2)A**
A	**4(0)**; **7(1)D**; **9(1)D**; 17(1)D; 18(1); **28(0)**; **29(1)**; **30(0)**; **31(1)**; **35(0)**; **37(1)**, **42(1)D**
B	10(0)D;16(1); **36(0)**; **40(1)**; 41(1)
C	**2(0)**; **6(1)**; 8(1)D; 14(0)AR; 19(1); **38(1)**
D	3(1); 5(0)AR; **21(0)A**; **22(0)**
E	28(1); 30(1)R
F	5(2)AR; 19(0)R; **24(1)D**
(*Ceratomontia argentina* + *C. brasiliana* + *C. centralis*)	**20(1)**
(*C. minor* + *C. tabulae*)	17(0); 39(0)
(*Monomontia brincki* + *M. corticola*)	2(1); 10(0)
(*Austromontia silvatica* + *A. bidentata*)	14(1); 34(1)
(*A. capensis* + (*M. lawrencei* + *M. rugosa*))	3(0)R
(*M. lawrencei* + *M. rugosa*)	2(2); 10(0); 11(0); 15(0)

species. The *Ceratomontia* species from South America constitute a clade that is the sister-group of the clade composed by the South African species of the ingroup. The analyses under implied weights resulted in the same tree with all concavities analyzed (Fig. 5), which is also one of the 12 trees obtained by the analysis under equal weights. For this reason, this is the hypothesis chosen to show and discuss the distribution and optimization of the characters.

The represented species of *Ceratomontia* and of the genera *Austromontia* and *Monomontia* comprise the monophyletic group (Fig. 5, A) with the highest support in the analysis: 94% bootstrap support and Bremer support of five. This clade is supported by ten unambiguous synapomorphies (eight in both optimizations, ACCTRAN and DELTRAN) such as the number of tarsomeres of tarsus I–IV (characters 28–30), the elongate dorsal plate of male genitalia (character 35, state 0) and the stylus of male genitalia enfolded by the dorsal plate (character 42, state 1). The clade formed by the South American *Ceratomontia* species (Fig. 5, B) is supported by two unambiguous synapomorphies, the entire ventral plate in male genitalia (character 36, state 0) and the number of male genitalia setae (character 40, state 1). This clade was supported by 83% of bootstrap replicates. The clade formed by the South African species of *Ceratomontia*, and the genera *Austromontia* and *Monomontia* (Fig. 5, C) is supported by three unambiguous synapomorphies including the shape of the ventral plate of the male genitalia, which is narrower in its basis than in the apex (character 38, state 1). This clade does not have a high support of bootstrap and Bremer support (49%, 1 respectively). The *Ceratomontia* species from South Africa appeared paraphyletic, basal in relation to the clade formed by the species of *Austromontia* and *Monomontia* (Fig. 5, E). This clade (E) is supported by two synapomorphies (a homoplasy and a reversal, respectively), the number of tarsomeres of tarsus I (character 28, state 1) and tarsus III and IV (character 30, state 1). Although recovered by the analyses under implied weights, this clade (E) was ambiguously supported by the analysis under equal weights. Some pairs of species appeared as clades in the analysis: *M. brincki* + *M. corticola*, *C. minor* + *C. tabulae* and *M. lawrencei* + *M. rugosa*.

DISCUSSION

The results show that *Ceratomontia* is indeed involved in a "Gondwanan relationship," although it includes other genera as it is not a monophyletic group. Because of these results, there are ways to interpret the classification: 1) consider all the species of the ingroup as a single genus, *Ceratomontia*, which has priority over the remaining genera; 2) consider the South African species of *Ceratomontia* (which includes the type species) and *Austromontia* and *Monomontia* species as *Ceratomontia* and describe a new genus for the South American species.

We are not making nomenclatural acts in the present paper although the clade formed by *Ceratomontia*, *Austromontia*, and *Monomontia* showed a high bootstrap support. We are aware that the case of this "intercontinental" genus is complex. To further clarify the relationships, an analysis with wider representation should be carried out, including more representatives of other genera in the family, especially those from the *Ceratomontia* group. Moreover, while the South American species of *Ceratomontia* (Fig. 5, B) showed reasonable support for description of a new genus, the South African species clade (Fig. 5, C) did not provide equal justification including the present species in one separate genus. Consequently, making nomenclatural changes based on the present analysis would result in a weakly supported *Ceratomontia*.

One example of the need of including more terminal taxa is the presence of a band of small granules on the ventral surface of the pedipalpal femur appearing as a synapomorphy of the ingroup (character 18, state 1). We know that this character state has a wider distribution as it is also present in other genera of the *Ceratomontia* group not included in the analysis. Besides, although coded as present for *C. brasiliana*, actually it is doubtful for the South American species of *Ceratomontia*. So it could be an eligible synapomorphy of a group formed only by some South African genera of Triaenonychinae.

It would also be necessary to include the type species of *Monomontia*, *M. atra* Lawrence 1931, which was not represented in the analysis due to lack of material and detailed descriptions, including male genitalia, in the literature. Therefore, any decision made now could bring more confusion to the case.

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Performance of two arboreal pitfall trap designs in sampling cursorial spiders from tree trunks

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Abstract. Tree trunks link the forest floor and higher canopy layers, thus constituting an important habitat element for many arthropod species, including spiders living in the canopy. We sampled spiders moving on tree trunks in the boreal forest using two trap designs referred to as "bottle traps" (BT) and "cup traps" (CT) placed on both trembling aspen (*Populus tremuloides* Michaux) and white spruce (*Picea glauca* (Moench) Voss) trees of similar DBH (diameter at breast height). Over an average of 83.5 ± 6.3 days/trap (48 traps), we collected a total 333 spiders, representing 13 families and 33 species. *Clubiona canadensis* Emerton 1890 (Clubionidae), *Callobius bennetti* (Blackwall 1846) (Amaurobiidae), *Pocadicnemis americana* Millidge 1976 (Linyphiidae), and *Orodrassus canadensis* Platnick & Shadab 1975 (Gnaphosidae) were the most commonly collected species, representing more than 60% of the total catch. Twenty eight species and 285 individuals were collected by BTs compared to 18 species and 48 individuals by CTs. Catches in BTs included 15 unique species, whereas five species were unique in CT catches. BTs are easier to transport and deploy, they catch more spiders per trap, and appear to more efficiently sample spider diversity. Thus we recommend the use of BTs to effectively sample wandering spiders on tree trunks; however, the use of both designs could increase understanding about the role of tree trunks as structural features linking forest canopies to the ground layers below.

Keywords: Sampling, arboreal fauna, Araneae, boreal forest, mixedwood, Canada

Tree trunks are an important structural feature in forest ecosystems because they link the forest floor and the canopy (Moeed & Meads 1983). Structural characteristics of trees affect the composition, abundance, and distribution of tree-dwelling organisms (Palik & Engstorm 1999). Tree bark is a key component for maintaining biodiversity in managed and unmanaged forests (Hanula et al. 2000); for example, habitat structural diversity provided by bark influences spider assemblages (Horvath et al. 2005), suggesting that this complexity is correlated with abundance of predators (Langellotto & Denno 2004). Recent studies have shown that high species richness of lichens on spruce trees positively influenced spider species richness (Gunnarsson et al. 2004). In addition, tree bark provides shelter for overwintering arthropods (Pekar 1999), and provides resting places or habitat islands for arthropods that are dispersing across habitats (Proctor et al. 2002).

Sampling techniques developed to collect arthropods moving on and inhabiting tree trunks include stem-eclectors (Funke 1971), emergence traps (Glen 1976), arboreal photo-eclectors (Moeed & Meads 1983), vacuum samplers (Nicolai 1986), branch traps (Koponen et al. 1997; Koponen 2004), corrugated cardboard bands (Pekar 1999; Isaia et al. 2006), time stem-eclectors (Simon et al. 2001), intercept traps (Majer et al. 2003), sticky traps (Basset et al. 2003), polyethylene bubble wraps (Roberts & Roberts 1988; Isaia et al. 2006), artificial shelters (Hodge et al. 2007), among many others (Basset et al. 1997; Szinetar & Horvath 2005). Some of these techniques are especially well-suited for sampling certain arthropod groups in relation to their activity patterns or microhabitat associations; others are expensive and difficult to transport or operate under field conditions. Some of these traps are effective for collecting spiders in trees (e.g., branch traps, corrugated cardboard bands) but generally particular traps target only some groups (e.g., foliage-dwelling spiders, under bark-dwelling spiders). Overall, there is a lack of agreement about which trap designs are most suitable and appropriate for collecting arthropods associated with tree bark. As a consequence, knowledge about the arthropod fauna inhabiting tree trunks remains preliminary (Roberts & Roberts 1988), although we are starting to understand species composition and habitat/microhabitat associations for spiders (Szinetar & Horvath 2005).

In this paper we present two new designs for traps that are easy to transport and to set and operate to collect spiders on tree boles in the field. Deployment of these traps is cost effective, allowing use of many traps so as to improve sampling effort and reliability of resulting data (Churchill & Arthur 1999). Additionally, we compared trap performance (in terms of spider abundance and richness) between these trap designs. Furthermore, we report a small experiment to estimate the variation in spider species composition between trunks of two common tree species in the mixedwood boreal forest.

METHODS

Study Site, Experimental Design and Sampling.—Traps were deployed during the summer of 2006 at the Ecosystem Management Emulating Natural Disturbance (EMEND) field site located in the Clear Hills Upland, Lower Foothills Ecoregion of northwestern Alberta, Canada (56°46′13″N, 118°22′28″W). This region is covered by a mosaic of different successional stages of boreal mixedwood forest dominated by aspen (*Populus tremuloides* Michaux), balsam poplar (*P. balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*P. mariana* (Miller)). Two different traps designed to collect spiders moving on tree trunks (see below) were tested in three different stands of uncut mixedwood forest (minimum distance between stands ca. 3 km). In each stand, eight traps (four of each design) were placed on the boles of eight aspen and eight white spruce trees of similar DBH (diameter at breast height) selected haphazardly, for a

total of 16 traps per stand. Trees sampled were at least 10 m apart and traps were all placed 2 m from the ground.

Spiders were collected from the traps in four collection periods at 3-wk intervals from 28 May to 24 August 2006 and preserved in 70% ethanol. Specimens were sorted and adult individuals were identified to species using relevant literature (Dondale & Redner 1978, 1982, 1990; Platnick & Dondale 1992; Dondale et al. 2003; Paquin & Dupérré 2003; Ubick et al. 2005), nomenclature followed the World Spider Catalog V8.5 (Platnick 2008). Voucher specimens are presently held in the Spence laboratory collection (Department of Renewable Resources, University of Alberta).

Trap Design.—"Bottle Traps" (BTs) were inverted 2 liter pop bottles (11.1 cm diameter) with the bottoms removed (Fig. 1a). These were stapled to the surface of the trees to be sampled. "Cup Traps" (CTs) consisted of 20 × 20 cm heavy plastic board sheets stapled to the sample trees, each sheet fitted with a 4 oz plastic cup; a 4.1 cm diameter opening for the cup was cut in the center of each board and a string attached to the distal edge of the board was stapled to the tree to maintain the trap in a horizontal position (Fig. 1b). A 5 × 20 cm plastic strip was placed on each side of traps of both designs, acting as a fence to direct spiders into the devices. Silicate-free ethylene glycol was used as a preservative in both kinds of traps.

Data Analysis.—Captures from each trap were pooled over the entire sampling period, and abundance of each species was standardized to spiders/day to adjust for uneven sampling resulting from animal disturbance. It has been suggested that trap perimeter affects catch (Luff 1975; Work et al. 2002). Thus, to test if differences in spider catch can be simply explained by trap perimeter or reflect actual trap performance, both standardized abundance and richness values were adjusted for trap perimeter, dividing these parameters by the trap circumference (BT = 34.87 cm; CT = 12.88 cm). Both non-adjusted and adjusted standardized values were compared.

Trap performance was assessed comparing standardized abundance and richness using rarefaction estimates with non-standardized abundances (Magurran 1988). Differences between trap designs, tree species, forest stands, and the interaction of these variables were analyzed for both adjusted and non-adjusted standardized abundance and richness values using factorial analyses of variance (ANOVA, $\alpha = 0.05$) in R (R Development Core Team 2007), using the CAR package (Fox 2007). Rarefaction estimates were calculated in R (R Development Core Team 2007) using the VEGAN package (Oksanen et al. 2007). In addition a post hoc power analysis ($\alpha = 0.05$) (Cohen 1988) was carried out in R (R Development Core Team 2007) using the PWR package (Champley 2007) for each factor (stand, tree species, trap design) with adjusted and non-adjusted data to determine the probability of Type II error and thus, determine if sample size was sufficient to support conclusions.

←

Figure 1.—Arboreal pitfall trap designs. a. Bottle Trap design (BT). b. Cup Trap design (CT). For details see text.

RESULTS

Over the four collections, 4.7% of the traps were disturbed by animals (six traps in the first collection and three in the second) and six traps (all CTs) collected no spiders throughout the sampling period. Thus, sampling effort averaged 83.5 ± 6.3 days/trap. In total, 13 families, 33 species and 333 individuals (Table 1) were captured. *Clubiona canadensis* Emerton 1890 (Clubionidae), *Callobius bennetti* (Blackwall 1846) (Amaurobiidae), *Pocadicnemis americana* Millidge 1976 (Linyphiidae), and *Orodrassus canadensis* Platnick & Shadab 1975 (Gnaphosidae) were the most abundantly collected species, collectively representing more than 60% of the total catch. Each of the remaining species in the catch was represented by fewer than 17 individuals.

Trap performance.—Both adjusted and non-adjusted standardized abundances and richness differed significantly between trap designs (Abundance: df = 1, 42 (for all comparisons of trap design), adjusted F = 19.19, P < 0.0001; non-adjusted F = 61.80, P < 0.0001. Richness: adjusted F = 4.17, P = 0.049; non-adjusted F = 91.46, P < 0.0001), suggesting higher abundance and richness in BTs. In addition, our analyses detected no significant differences in standardized abundance for either adjusted or non-adjusted data between tree species (df = 1, 42 (for all comparisons of tree species), adjusted F = 1.20, P = 0.29; non-adjusted F = 0.47, P = 0.49); however, richness adjusted values showed significant difference (F = 4.31, P = 0.045), indicating a slight higher adjusted richness in white spruce, however non-adjusted values showed no difference (F = 1.32, P = 0.26). Likewise, catch did not vary significantly among stands with respect to either abundance (df = 2, 42 [for all comparisons of stands], adjusted data F = 1.77, P = 0.19; non-adjusted F = 1.08, P = 0.35) or richness (adjusted F = 3.0764, P = 0.058; non-adjusted F = 2.50, P = 0.10). There was no significant interaction between trap design and tree species for abundance (df = 1, 42 [for all comparisons of interaction of tree species and trap design], adjusted F = 0.2508, P = 0.62; non-adjusted F = 4.074e-06, P = 0.998) and for the non-adjusted richness data (F = 1.32, P = 0.26). However, this "design × trap" interaction was significant for the adjusted richness values (F = 4.31, P = 0.045). Power analysis showed that the probability of Type II error in these comparisons is less than 0.01 for both adjusted and non-adjusted data.

BTs collected an average of 11.88 ± 1.18 spiders and 5.83 ± 0.42 species per trap in contrast to CTs that collected an average of 2.00 ± 0.35 spiders and 1.67 ± 0.25 species per trap. Thirteen species were collected in traps of both designs accounting for 39.4% of the total catch; BTs captured 15 unique species as compared to five unique species in CTs. An average of 7.54 ± 1.43 spiders and 4.00 ± 0.48 species were collected per trap on spruce trees, whereas in aspen an average of 6.33 ± 1.25 spiders and 3.30 ± 0.62 species were collected per trap. Eighteen species were observed on both spruce and aspen trees and these accounted for 54.6% of the total catch. Eight species were collected only on spruce and eight species only on aspen.

These results indicate that BT samples had both higher abundance and richness (Fig. 2) and this supports the use of this trap for assessing the spider fauna that is moving along tree trunks. However, rarefaction curves indicate that CTs collect a higher number of species based on the same number of individuals (Fig. 2).

Bark-dwelling spider assemblages in the boreal forest.—According to data about habitats in which the species in our traps were previously collected (Table 1), and to the habitat association classification proposed by Wunderlich (1982), 11 species can be characterized as accidental, three species as either accidental or facultative, eight as facultative, and two as either facultative or exclusive.

DISCUSSION

Trap performance.—In general, spider catch was low considering the number of traps placed in each forest stand. Spiders use tree bark only temporarily (Horvath et al. 2005) and our results suggest that spider activity is low on tree trunks. We remain convinced, however, that these trap designs provide reasonable samples of spider assemblages using the bole as habitat. The relatively high abundance of *C. canadensis*, which is generally associated with tree bark (Dondale & Redner 1982), and *C. bennetti*, which is a typical bark-dwelling spider, suggests that traps of both designs actually collect a representative fauna from this habitat.

Performance of BTs and CTs differed significantly, although the significance of the trap design effect is marginal for species richness adjusted for trap perimeter. This suggests that differences in abundance in fact reflect differences in trap efficiency but that differences in richness might be confounded by the low number of species observed in the tree bark habitat. Nonetheless, BTs collected six times more spiders and almost twice as many species as did CTs, in fact, six out of 24 CTs collected no spiders. Less than half of the species recorded were collected in both traps (13 spp.) and in general these were more abundant in BTs (Table 1). In addition, a large proportion of species were collected only in BTs but few species were unique to CTs. Abundances of species unique to one trap design were very low, mainly singletons and doubletons. *Cryphoeca montana* Emerton 1909 (Hahniidae) was the most abundant of these unique species (8 individuals, Table 1).

The better performance of BTs is probably due mainly to how they work. The opening of a BT is in direct contact with the tree bark (Fig. 1a) and, thus, there is higher probability that spiders will crawl into the device than first crawling out onto the horizontal platform (Fig. 1b) and then into a cup. At a low level of overall activity, differences in catch between CTs and BTs could be highly significant to the quality of faunal assessment achieved. Despite a clear difference in quantitative performance in favor of BTs, rarefaction curves suggest that under a similar sampling effort CTs collect more species. However, to collect a comparable number of species and individuals as in BTs, considerably more sampling effort must be expended using CTs.

Given the above results, we recommend use of BTs to effectively sample wandering spiders on tree trunks. In addition to performing well, BTs are easy to set and transport in the field. They are also cost effective; 2 liter plastic pop bottles can be purchased inexpensively in high quantities in any recycling center. The combination of species characteristics and microhabitat affinities inevitably biases any trap catch. Thus, we also recommend that other sampling

Table 1.—Total spider abundance by tree species and trap design and habitat association in a mixedwood forest in northwestern Alberta, Canada. Trap design: BT= Bottle Trap, CT= Cup Trap. Habitat Association: E=Exclusive, F=Facultative, A=Accidental.

Family	Species	*Picea glauca*		*Populus tremuloides*		Total	Habitat association	References for habitat association
		BT	CT	BT	CT			
Agelenidae	*Agelenopsis utahana* (Chamberlin & Ivie 1933)	3	2	2		7	A	(Lowrie 1948; Jennings et al. 1988; Buddle 2001)
Amaurobiidae	*Amaurobius borealis* Emerton 1909	1	1	2		4	A	(Jennings et al. 1988; Buddle 2001; Varady-Szabo & Buddle 2006)
	Callobius bennetti (Blackwall 1846)	48	2	17	1	68	A, F	(Szinetar & Horvath 2005; Varady-Szabo & Buddle 2006)
	Callobius nomeus (Chamberlin 1919)			1		1	A, F	(Aitchison-Benell & Dondale 1990)
Araneidae	*Araneus* sp1			1		1	—	—
	Araneus sp2		1			1	—	—
	Araniella displicata (Hentz 1847)	2				2	A	(Jennings & Collins 1986; Jennings & Dimond 1988; Jennings et al. 1990; Dondale et al. 2003)
	Cyclosa conica (Pallas 1772)	2	2	2		6	A	(Dondale et al. 2003)
Clubionidae	*Clubiona canadensis* Emerton 1890	24	2	44	6	76	F	(Dondale & Redner 1982; Jennings & Dimond 1988; Jennings et al. 1988; Buddle 2001)
	Clubiona moesta Banks 1896			1		1	F, E	(Dondale & Redner 1982; Buddle 2001)
Dictynidae	*Dictyna brevitarsa* Emerton 1915				1	1	F	(Jennings & Collins 1986; Jennings & Dimond 1988; Jennings et al. 1988; Jennings et al. 1990)
	Emblyna annulipes (Blackwall 1846)				1	1	A	(Hagley & Allen 1989)
Gnaphosidae	*Orodrassus canadensis* Platnick & Shadab 1975	14	2	9	1	26	F	(Jennings & Collins 1986; Jennings et al. 1988; Platnick & Dondale 1992)
Hahniidae	*Cryphoeca montana* Emerton 1909	5		3		8	A	(Koponen 1987; Jennings et al. 1988; Larrivee et al. 2005; Varady-Szabo & Buddle 2006)
Linyphiidae	*Drapetisca alteranda* Chamberlin 1909	1				1	F	(Buddle 2001)
	Estrandia grandaeva (Keyserling 1886)		1		1	2	F	(Pettersson 1996)
	Incestophantes calcaratus (Emerton 1909)	5	4	6	1	16	—	—
	Pityohyphantes costatus (Hentz 1850)	2	1	2		5	A	(Jennings & Collins 1986; Jennings & Dimond 1988)
	Pityohyphantes subarticus Chamberlin & Ivie 1943	2	3	1		6	—	—
	Pocadicnemis americana Millidge 1976	19	6	21	2	48	F	(Jennings & Dimond 1988; Jennings et al. 1988; Larrivee et al. 2005)
	Walckenaeria auranticeps (Emerton 1882)			2		2	—	—
Liocranidae	*Agroeca ornata* Banks 1892	3				3	A	(Dondale & Redner 1982; Koponen 1987; Buddle et al. 2000; Varady-Szabo & Buddle 2006)
Lycosidae	*Pardosa mackenziana* (Keyserling 1877)	1				1	A	(Dondale & Redner 1990; Buddle 2000; Buddle et al. 2000; Buddle 2001)
Philodromidae	*Philodromus pernix* Blackwall 1846	3		1		4	F, E	(Lowrie 1948; Dondale & Redner 1978; Jennings & Dimond 1988; Jennings et al. 1990)
	Philodromus placidus Banks 1892	3	1	2	1	7	F	(Dondale & Redner 1978; Jennings & Collins 1986; Jennings & Dimond 1988; Jennings et al. 1990)
	Philodromus rufus quartus Dondale & Redner 1968	1				1	F	(Dondale & Redner 1978; Jennings & Collins 1986; Jennings & Dimond 1988)
Salticidae	*Pelegrina flaviceps* (Kaston 1973)				1	1	—	—
	Pelegrina flavipes (Peckham & Peckham 1888)	1				1	—	—
	Sitticus finschi (L. Koch 1879)	1		1		2	—	—
Theridiidae	*Enoplognata intrepida* (Sørensen 1898)	3				3	—	—
	Theridion montanum Emerton 1882	5	1	8	2	16	A, F	(Jennings & Collins 1986; Jennings & Dimond 1988; Jennings et al. 1988)
Thomisidae	*Xysticus canadensis* Gertsch 1934	1	1	7		9	A	(Dondale & Redner 1978; Jennings et al. 1988; Pearce et al. 2004; Larrivee et al. 2005)
	Xysticus obscurus Collett 1887	1		1		2	A	(Dondale & Redner 1978; Koponen 1987)
Total		151	30	134	18	333		

techniques should be employed while we are developing a more mature understanding of bark-dwelling spider species. Both trap designs introduced here can contribute to these efforts.

Bark-dwelling spider assemblages in the boreal forest.— Trunks of white spruce trees are structurally more complex than are those of trembling aspen. For example, spruce trees have more branches and these carry needles, even near to the ground, while aspen branches are restricted to higher layers of the canopy. In addition bark of spruce trees is of much rougher texture than is that of aspen. More microhabitats appear to be available on spruce tree boles and, thus, one might expect these to harbor a more diverse assemblage of bark-dwelling spiders. Even though most of our analyses demonstrated no significant effect of tree species on the spider catch, we did detect a significant but weak difference between tree species using richness values adjusted for trap perimeter. Nonetheless, the lack of apparent difference between catches on these two tree species with considerably different habitat quality suggests that most spiders captured on living tree trunks are using the boles mainly as movement corridors, rather than as habitat.

Bark-dwelling spiders have been classified according to how strongly connected they are to this habitat (Wunderlich 1982) as follows: 1) Exclusive bark-dwellers are species that live on or under the bark during all or most part of their life cycle; 2) Facultative bark-dwellers are species that typically, but not exclusively, use this habitat; and 3) Aceidental species are typically from other habitats and use bark habitats by chance or as an alternative. According to Szinetar & Horvath (2005) of the 289 European species that have been recorded in tree trunks, 65% are accidental species, 27% are facultative species, and only 8% are exelusive bark-dwellers. In North America information on bark-dwelling species is scarce and scattered (e.g., Lowrie 1948; Bennett 2001; Buddle 2001; Holmberg & Buckle 2002); in particular, little is known about spider composition on tree trunks in the boreal forest, and thus habitat associations are difficult to determine.

Given the information available about habitat associations for species collected during the present study, we identify a similar trend in the boreal forest to that above: we found a higher proportion of accidental species and a lower proportion of facultative or exclusive speeies (Table 1). One third of the total number of species can be characterized as accidental species on tree bark, whereas only a few species could be categorized as facultative and/or exclusive, supporting the idea that most of the species present in tree trunks are using this habitat temporarily and that only a few species are true bark-dwellers. Although these species represent a small part of the overall fauna (standing dead trees were not included in this study), those species that are facultative or exclusive in use of trunk habitats should be considered as significant biodiversity components, especially if there are species associated with standing dead trees.

Further research should be focused on the role of bark-dwelling spider assemblages in the boreal forest, especially those dependent on dead trees. Buddle (2001), for example, showed that spider assemblages collected directly from downed woody material (DWM) are highly similar to assemblages collected on the forest floor. Our work supports

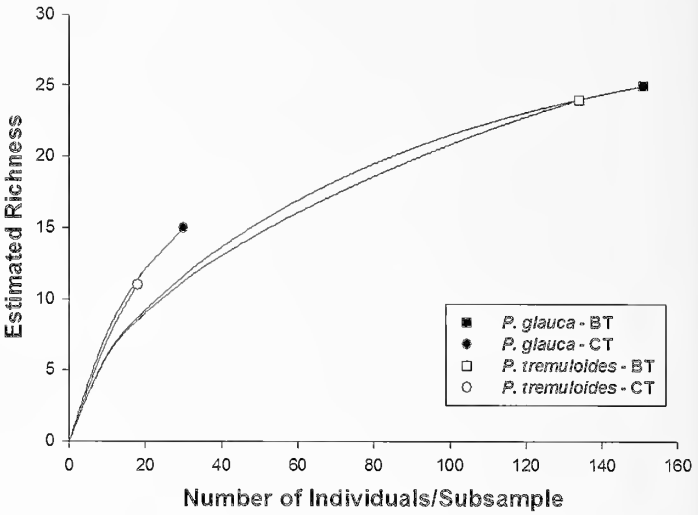

Figure 2.—Rarefaction curves for two arboreal pitfall trap designs in *P. glauca* and *P. tremuloides* trees in a mixedwood forest. BT: Bottle Trap design, CT: Cup Trap design.

a similar conclusion because many of the species colleeted in BTs and CTs are also common either on the foliage (J. Pinzon, unpublished data) or on the forest floor (Dondale & Redner 1978, 1982; Buddle 2001). However, little is known about the spider composition on dead standing trees in the boreal forest; as a consequence, at this point, it is difficult to determine if specialists inhabit this habitat or if the species composition in dead standing trees is comparable to that in living trees.

One set of species commonly found on tree trunks are not exclusively bark-dwellers beeause they are common in other habitats, such as forest litter and foliage (e.g., *Agelenopsis utahana* (Chamberlin & Ivie 1933) (Agelenidae), *Amaurobius borealis* Emerton 1909 (Amaurobiidae), *C. canadensis*, *O. canadensis*, *Pityohyphantes costatus* (Hentz 1850) (Linyphiidae)). Sueh species could use tree boles either as a connection between the forest floor and higher layers of the forest, as a suitable place for mating, foraging for food, or for hiding from predators. This study provides new trap designs for exploring the fauna of spiders using tree trunks. In addition some information regarding bark dwelling spiders in the boreal forest is presented, however these traps could be used in any kind of forest. Using BTs to thoroughly sample this type of habitat for spiders will increase understanding of the role of tree trunks and standing dead trees as habitats and struetural features for spider assemblages as components of biodiversity in forested ecosystems.

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The scorpion genus *Ananteris* in Colombia: comments on the taxonomy and description of two new species (Scorpiones, Buthidae)

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Abstract. Two new scorpion species are described from Colombia: *Ananteris arcadioi* sp. nov. from Meta Department and *Ananteris dorae* sp. nov. from Nariño Department. These new species raise to 62 the number of known species of *Ananteris*, eight of which are found in Colombia. Some comments on the taxonomy of Colombian *Ananteris* are included and some characters are proposed to define species whereas the usefulness of others is briefly discussed. A map with the known distribution of the different species in Colombia, a table for some characters, and a key for the identification of the Colombian species of the genus are included.

Keywords: Scorpions, taxonomy, Colombia

The genus *Ananteris* Thorell 1891 is a group of scorpions with a Gondwanan distribution (Lourenço 1985), currently known from 60 species mostly from Venezuela and Brazil (González-Sponga 2006; Kovarík 2006; Lourenço et al. 2006; Botero-Trujillo 2007; Teruel & García 2007). Until recently six species had been recorded from Colombia: *A. columbiana* Lourenço 1991, *A. ehrlichi* Lourenço 1994, *A. gorgonae* Lourenço & Flórez 1989, *A. leilae* Lourenço 1999, *A. myriamae* Botero-Trujillo 2007 and *A. tolimana* Teruel & García 2007 (Flórez 2001a; Lourenço et al. 2006; Botero-Trujillo 2007; Teruel & García 2007). Botero-Trujillo (2007) indicated that other specimens were under study, among which two new species were identified and are described in the present paper raising to eight the number of Colombian species of *Ananteris*. The results presented herein give evidence that the inventory work of this genus in Colombia is far from completed, and reveal that further collecting and exploration is needed to reach more precise approximations of the distribution and diversity of this poorly known genus in the country.

HISTORY OF COLOMBIAN *ANANTERIS*

The genus *Ananteris* was first recorded in Colombia by Hummelinck (1940), who recorded a juvenile female of *A. cussinii* Borelli 1910 in the city of Riohacha (La Guajira Department); however, only three species of *Ananteris* were known at that time, and that author did not provide enough information regarding the morphology of his specimen to reliably support its specific identity. The characters he did use are now known to be uninformative either due to their variability (i.e., number of pieces in the middle lamellae of the pectines) or because they are present in most species of the genus (i.e., five carinae in metasomal segment V). Consequently, later authors mentioned the presence of this species in Colombia (Flórez 1990; Flórez & Sánchez 1995; Fet & Lowe 2000; Prendini 2001); however, in Flórez's (2001a) recent catalogue of Colombian scorpions of the family Buthidae *A. cussinii* is not included, and Flórez (2001b) considered the specimen mentioned by Hummelinck (1940) to be probably *A. columbiana* and, therefore, indicated a need for a revision. The specimen is deposited in the Zoological Museum of the State University, Utrecht, Netherlands.

Lourenço & Flórez (1989) described *A. gorgonae* on the basis of a male from Isla Gorgona, becoming the first species to be described from Colombia. Later contributions provided descriptions of *A. columbiana* [previously thought to be *A. ashmolei* Lourenço 1981 (Lourenço 1982:138)], *A. ehrlichi*, *A. leilae*, *A. myriamae*, and *A. tolimana*. Of these, only *A. columbiana* and *A. tolimana* are known from both sexes, whereas the female of *A. gorgonae* and the male of the others remain unknown (Lourenço & Flórez 1989; Lourenço 1991, 1994, 1999a; Botero-Trujillo 2007; Teruel & García 2007).

In the original descriptions of *A. gorgonae*, *A. columbiana*, *A. ehrlichi*, and *A. leilae* the diagnoses provided are not detailed enough. In those of *A. gorgonae* and *A. leilae* it is only indicated that these species can be distinguished from their closest relative (*A. ashmolei* and *A. gorgonae*, respectively) based on the number of pectinal teeth; no other characters are provided, not even characters shared by both species (see Lourenço & Flórez 1989; Lourenço 1999a). The description of *A. ehrlichi* mentions that it can be distinguished from *A. ashmolei* due to differences in the coloration of the pedipalp chelae and different morphometrie values, once more without mention of the features shared (see Lourenço 1994). Finally, the description of *A. columbiana* lacks a diagnosis or a comparative section with other species (see Lourenço 1991).

METHODS

Illustrations were prepared with the aid of a *camera lucida* mounted onto a Zeiss Stemi SV 6 stereoscope. Measurements (L = length, W = width, D = depth) are presented in millimeters and were obtained following the methodology of Sissom et al. (1990), using the program Motic Images 2000 version 1.2 through a PC connected to a Motic Digital Microscope DM-143. The distribution map was produced with the program ArcView GIS version 3.1 [Environmental Systems Research Institute (ESRI), Redlands, California]. All specimens are preserved in 70% ethanol.

General carinal terminology follows Vachon (1952), except for the mesosomal carinae that are here distinguished as follows. In the tergites: axial, dorsolateral and lateral carinae; in the sternites: paramedian and lateral carinae. Vachon's (1952:fig. 65) term ventrointernal to denote the carina that follows the dorsointernal on pedipalp femur is here replaced

for internal median, since in the specimens studied herein there is an additional and more ventral carina to which the term ventrointernal is more suitable. Trichobothrial terminology follows Vachon (1973, 1975).

The specimens examined for this study are lodged in the following museums: Museo Javeriano de Historia Natural "Lorenzo Uribe S. J.", Pontificia Universidad Javeriana, Bogotá, Colombia (MPUJ); Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia (ICN-MHN); Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia (IAvH). In the course of this study, a number of specimens of *Ananteris* were examined apart from the two new species. These specimens are detailed below:

Ananteris columbiana: COLOMBIA: *Atlántico Department*: 1 ♀, Puerto Colombia, El Nisperal, 10°59′28″N, 74°57′43″W, 100 m elev., 10–15 June 2006, G. Fagua (MPUJ-SCO-334); *Bolívar Department*: 1 ♀, Cartagena, Isla Barú, 10°23′59″N, 75°30′52″W, 40 m elev., pitfall, 14 October 2006 (MPUJ-SCO-358); 1 ♂, Zambrano, Hacienda Monterrey, 09°45′N, 74°49′W, 70 m elev., 01 December 1997, F. Fernandez & G. Ulloa (ICN-MHN-As-446); 1 juvenile, Zambrano, Hacienda Monterrey, 09°45′N, 74°49′W, 120 m elev., dry forest, pitfall, August 1996, F. Escobar (ICN-MHN-As-176); 1 ♀, Zambrano, Hacienda Monterrey, 09°45′N, 74°49′W, 70 m elev., 19 October 1993, F. Fernandez (ICN-MHN-As-595); 1 ♀, Zambrano, 09°45′N, 74°49′W, 20 m elev., 25 August 1992, A. Molano (ICN-MHN-As-111); 1 juvenile, Santa Catalina, Hacienda El Ceibal, 10°36′N, 75°18′W, 20 m elev., October 1999, E. Flórez & biology students (ICN-MHN-As-294); 1 ♀, Parque Nacional Natural Colorados, La Yaya, 09°54′N, 75°07′W, 280 m elev., pitfall, 24–26 May 2001, E. Deulufeut, M. 1731 (IAvH-E 100770); 1 ♀, Parque Nacional Natural Colorados, Alto El Mirador, 09°54′N, 75°07′W, 400 m elev., pitfall, 5–9 July 2001, E. Deulufeut, M. 1956 (IAvH-E 100771); 1 ♀, Parque Nacional Natural Colorados, Alto El Mirador, 09°54′N, 75°07′W, 400 m elev., pitfall, 2–6 December 2001, E. Deulufeut, M. 2644 (IAvH-E 100772); 1 ♀, Parque Nacional Natural Colorados, La Suiris, 09°54′N, 75°07′W, 126 m elev., pitfall, 18–21 November 2000, E. Deulufeut, M. 937 (IAvH-E 100773); 1 ♀, Parque Nacional Natural Colorados, La Suiris, 09°54′N, 75°07′W, 126 m elev., pitfall, 18–20 December 2000, E. Deulufeut, M. 976 (IAvH-E 100774); 1 ♀, Parque Nacional Natural Colorados, Villa Roca, 09°54′N, 75°07′W, 180 m elev., pitfall, 19–22 August 2001, E. Deulufeut, M. 2055 (IAvH-E 100775); 1 juvenile [♂ (?)], Parque Nacional Natural Colorados, Villa Roca, 09°54′N, 75°07′W, 180 m elev., pitfall, 24–26 May 2001, E. Deulufeut, M. 1729 (IAvH-E 100776). *Córdoba Department*: 1 ♂, Pueblo Nuevo, Hacienda Toronto, 08°30′N, 75°31′W, 30 m elev., 7–13 June 2004, J. D. Lynch (ICN-MHN-As-585); *Magdalena Department*: 1 ♂, 1 ♀, Santa Marta, Parque Nacional Natural Sierra Nevada de Santa Marta, 11°15′N, 74°12′W, 120 m elev., December 2006, J. A. Noriega (MPUJ-SCO-363, 364); 1 ♀, Santa Marta, near Quebrada Minca, 11°15′N, 74°12′W, 2 m elev., November 1976 (ICN-MHN-As-121); 1 ♀, Parque Nacional Natural Tayrona, Zaino, 11°20′N, 74°02′W, 50 m elev., pitfall, 4–6 December 2000, H. Henriquez, M. 1013 (IAvH-E 100777); 1 ♀, Parque Nacional Natural Tayrona, Pueblito, 11°20′N, 74°02′W, 225 m elev., pitfall, 30 September 2000, H. Henriquez, M. 660 (IAvH-E 100778); 2 ♀, Parque Nacional Natural Tayrona, Pueblito, 11°20′N, 74°02′W, 225 m elev., pitfall, 29 July 2000, H. Henriquez (IAvH-E 100779,100780); 1 juvenile [♂ (?)], Parque Nacional Natural Tayrona, Pueblito, 11°20′N, 74°02′W, 225 m elev., pitfall, 15 August 2000, H. Henriquez (IAvH-E 100781).

Ananteris ehrlichi: COLOMBIA: *Caquetá Department*: 1 ♀, La Montañita, Santuario Las Iglesias, Itarca, 01°29′N, 75°26′W, 330 m elev., 25 April 2004, M. Agudelo (ICN-MHN-As-579); 1 ♀, Parque Nacional Natural Chiribiquete, Río Mesay, 0°47′N, 72°48′W, 20 January 2000, F. Quevedo (ICN-MHN-As-361); 1 ♀, Parque Nacional Natural Chiribiquete, Río Sararamano, 0°47′N, 72°48′W, April 2000, F. Quevedo (ICN-MHN-As-342).

Ananteris gorgonae: COLOMBIA: *Cauca Department*: 1 ♂, Parque Nacional Natural Gorgona, El Mirador, 02°58′N, 78°11′W, 180 m elev., , pitfall, 3–4 February 2001, R. Duque (ICN-MHN-As-427); 1 ♂, Parque Nacional Natural Gorgona, El Helechal, 02°58′N, 78°11′W, 30 m elev., 02°58′N, 78°11′W, pitfall, 17–19 July 2001, H. Torres, M. 2003 (IAvH-E 100766); 1 ♂, Parque Nacional Natural Gorgona, Alto El Mirador, 02°58′N, 78°11′W, 180 m elev., 02°58′N, 78°11′W, pitfall, 18–20 January 2001, H. Torres, M. 1245 (IAvH-E 100767); 1 ♂, Parque Nacional Natural Gorgona, El Helechal, 02°58′N, 78°11′W, 30 m elev., 02°58′N, 78°11′W, pitfall, 8–9 March 2002, H. Torres, M. 3098 (IAvH-E 100768); 1 adult [gynandromorph (?)], Parque Nacional Natural Gorgona, El Roble, 02°58′N, 78°11′W, 130 m elev., 02°58′N, 78°11′W, pitfall, 20–21 February 2001, H. Torres, M. 1369 (IAvH-E 100769).

Ananteris aff. *gorgonae:* COLOMBIA: *Valle del Cauca Department*: 1 ♀, Buenaventura, Bahía de Malaga, Base Naval, 03°54′N, 77°04′W, 5 m elev., April 1989, L. A. Millan (ICN-MHN-As-391).

Ananteris leilae: COLOMBIA: *Chocó Department*: ♀ holotype, Riosucio-La Gira, 07°26′N, 77°07′W, 20 m elev., July 1992, L. Mendoza & C. Torres (ICN-MHN-As-110); 1 ♂, Acandí, Capurganá, Los Ríos, 08°31′N, 77°16′W, 230 m elev., 25 April 2007, M. Gutierrez (MPUJ-SCO-374); 1 ♀, Acandí, Capurganá, Jardín Botánico del Darién, 08°31′N, 77°16′W, 40 m elev., Rastrojo, 11 October 2007, C. Acosta, J. Alfonso & C. Cocoma (MPUJ-SCO-377).

Ananteris myriamae: COLOMBIA: *Meta Department*: ♀ holotype, Villavicencio, Vereda El Carmen, 04°09′N, 73°38′W, 850–1000 m elev., into forest, pitfall, 23 December 2005, M. Viola (MPUJ-SCO-245); ♀ paratype, Villavicencio, Vereda El Carmen, 04°09′N, 73°38′W, 850–1000 m elev., Río Caño Blanco, under litter, ad hoc, at night, 18 April 2005, R. Botero-Trujillo (MPUJ-SCO-039).

TAXONOMY

Family Buthidae Koch 1837
Genus *Ananteris* Thorell 1891

Ananteris Thorell 1891:65.

Type species.—*Ananteris balzanii* Thorell 1891, by original designation.

Ananteris arcadioi sp. nov.
Figs. 1–11; Tables 1, 2

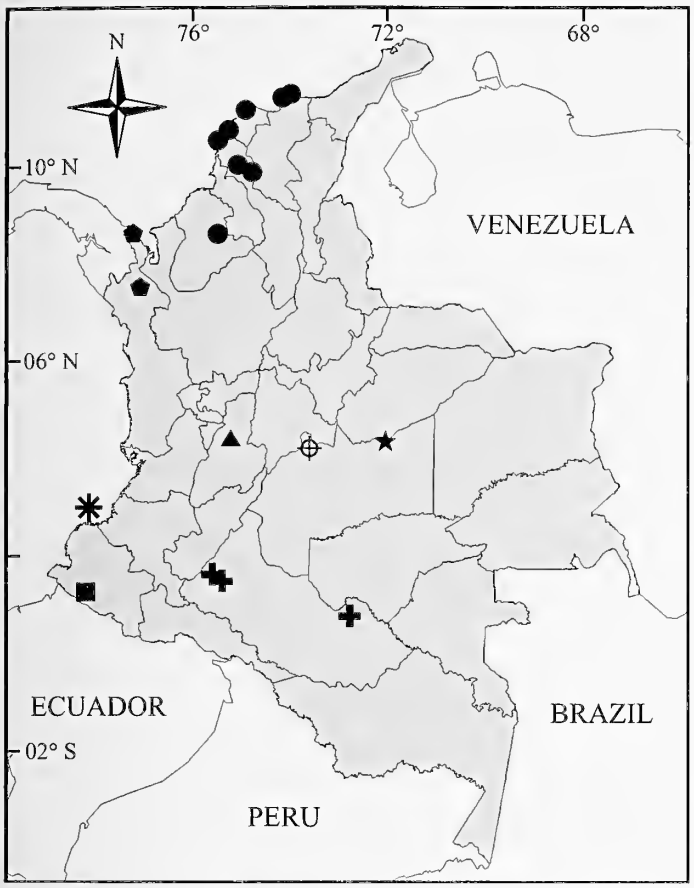


Figure 1.—Known distribution of Colombian *Ananteris*: *A. arcadioi* sp. nov. (✶); *A. columbiana* (●); *A. dorae* sp. nov. (■); *A. ehrlichi* (+); *A. gorgonae* (✻); *A. leilae* (⬟); *A. myriamae* (⊕); *A. tolimana* (▲). Note: Flórez's (2001a, 2001b) report of *A. gorgonae* in continental Colombia (Valle del Cauca Department) is not included, since the examination of his specimen (ICN-MHN-As-391) revealed that it could actually correspond to a different species.

Type material.—*Holotype:* COLOMBIA: *Meta Department*: adult male, Puerto Gaitán, Altamira, Club Los Llaneros, 04°19′N, 72°05′W, 140 m elev., into forest, ad hoc, at night, 19 October 2006, I. Gélvez (MPUJ-SCO-356).

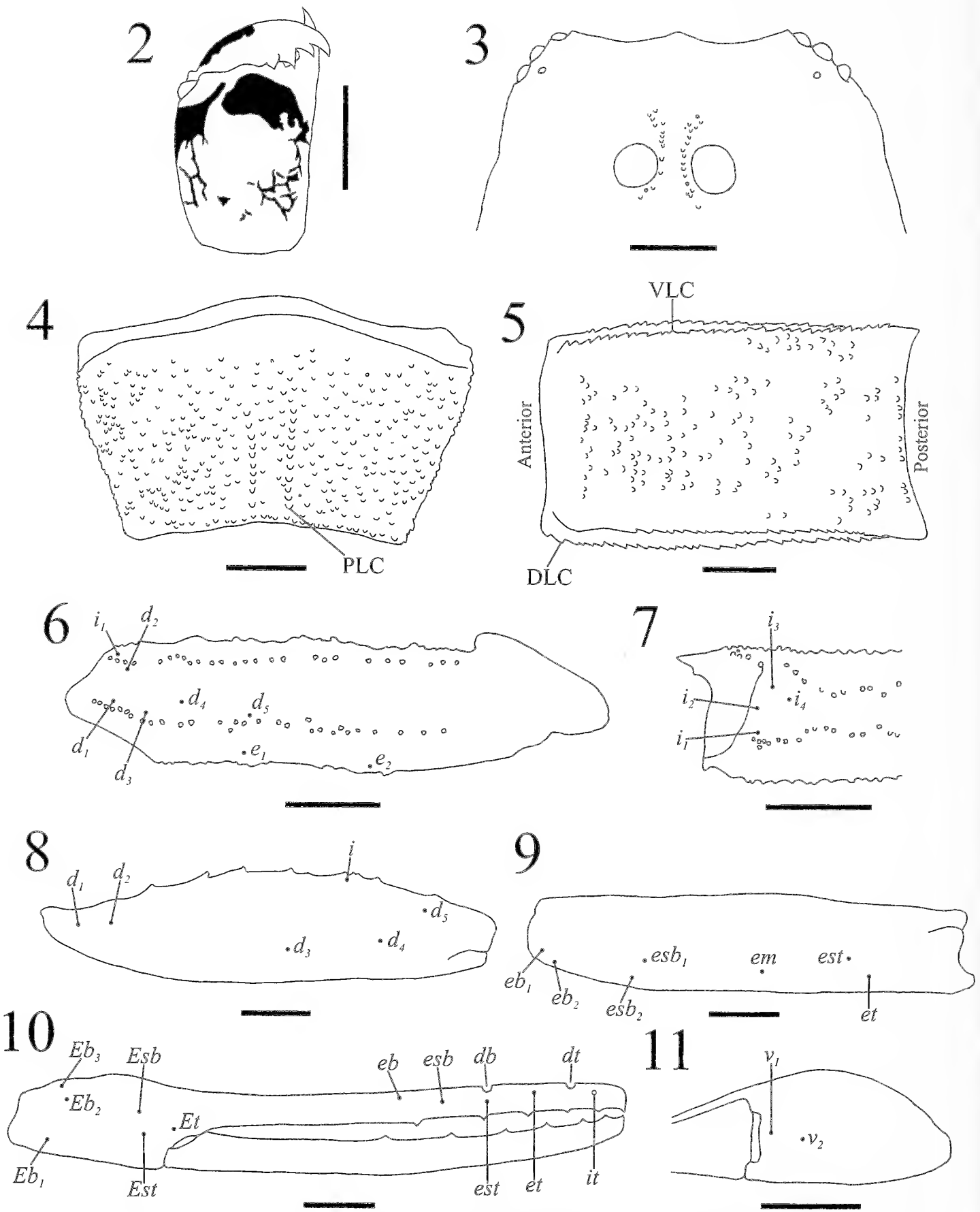
Etymology.—Patronym dedicated to the author's father, Arcadio Botero, in recognition of his great human quality, and acknowledgment of his unconditional support and encouragement.

Diagnosis (based on male only).—*Ananteris arcadioi* differs from all other species of the genus by the following unique combination of features: v_1 and v_2 trichobothria are not aligned axially but v_2 is located on an external position in relation to v_1 (Fig. 11); only *et* trichobothrium is located between *db* and *dt* on pedipalp fixed finger, and *est* is located beside *db* (Fig. 10); the carapace has a well developed anteromedian eminence (Fig. 3); the metasomal carinal formula is 10:10:10:6:5 with intermedian carinae on segment III only present anteriorly, and ventral and intermedian carinae absent on segment IV (Fig. 5); the dorsal surface of chelicerae exhibits a low degree of reticulation (Fig. 2); and pectines have 20–21 teeth.

Description based on male holotype (MPUJ-SCO-356).—*Coloration:* General coloration yellowish with variegated pigmentation over almost the entire body and appendages. Carapace predominantly brown with some yellow spots and bands; anterior and posterior margins brown; arising posterior to the lateral eyes there are two thin and almost straight yellow lines, each directed toward the midline but ending behind the median ocular tubercle; median ocular tubercle black, surrounded on its base by thin yellow lines on the anterior, anterolateral, and posterolateral margins. Chelicerae with coxa, hand, movable finger, and fixed finger yellowish; hand with a markedly incomplete reticular pattern in dorsal view (Fig. 2); fixed finger yellow with reddish teeth; movable finger with a dorsal brown area basally, teeth reddish. Coxosternal region, genital operculum, pectinal basal piece, peetines and sternites III–VI completely yellow; sternite VII with inconspicuous brown spots between the midline and the lateral margins; sternite V with a subtriangular posterior median hyaline area. Tergites predominantly brown; two longitudinal yellow lines crossing from tergites II to VI are only evident in the posterior half of each segment beside the midline; these lines are more conspicuous in tergites II–VI and appear as rounded spots in tergite I; each side of tergites I–VI with two transverse yellow lines converging near the longitudinal lines, arrow-like; tergite VII predominantly yellow, with brownish regions dorsally and laterally; lateral margins of tergites I–VII completely yellow. Metasoma predominantly yellow; dorsal intercarinal spaces of segments I–IV with a median brown design that is wider anteriorly, triangle-like in segments I–III; segments I–IV with variegated pigmentation in dorsal and lateral surfaces, ventral surfaces predominantly yellow; segment V reddish, with variegated darker pigmentation in all views. Telson reddish, darker than segment V and with inconspicuous brownish spots ventroexternally; aculeus dark red, yellowish basally; subaculear tubercle yellowish. Pedipalps predominantly brown; coxa and trochanter with variegated pigmentation; femur brownish with yellow areas on all surfaces, predominantly yellow ventrally, insertion of all the trichobothria surrounded by a rounded yellow area; patella with variegated pigmentation in dorsal and external surfaces, predominantly yellow internally and ventrally, insertion of all the trichobothria surrounded by a rounded yellow area; hand completely yellow dorsally and externally, with dark brown spotted areas internally and ventrally; fixed and movable fingers pale brown. Legs with variegated pigmentation, brown spots in all segments except for the telotarsus that is completely yellow.

Carapace: With very fine granulation throughout, and densely covered with greater but weak rounded granules especially in the brown areas; lateral margins not parallel; anterior margin with a well developed eminence (Fig. 3); ocular carinae evident, others inconspicuous; a median depression anterior to the ocular tubercle and a posterior median longitudinal furrow are evident; median ocular tubercle low, located in the posterior half of the anterior third of the carapace, with dense thin granulation and few greater granules; lateral ocular tubercles each with four ocelli, the posterior most is very reduced and unaligned with the remaining three pairs (Fig. 3).

Chelicerae: With abundant fine white setae on the internal and ventral surfaces; cheliceral dentition characteristic of the family Buthidae (Vachon 1963). Movable finger externally



Figures 2–11.—*Ananteris arcadioi* sp. nov., male holotype (MPUJ-SCO-356). 2. Dorsal view of the left chelicera; 3. Anterior margin of the

Table 1.—Variation of the pectinal teeth number in all species of Colombian *Ananteris*. Data of type specimens not studied were taken from the original descriptions and are included. N = number of pectines.

Species	Sex	N	Pectinal teeth number												Mean	Mode
			13	15	16	17	18	19	20	21	22	23	24	25		
A. arcadioi	♂	2							1	1					20.5	—
A. columbiana	♀	34		2	5	15	11	1							17.12	17
	♂	8			2	1	5								17.38	18
A. dorae	♀	2	2												13	—
A. ehrlichi	♀	8								3	4	1			21.75	22
A. gorgonae	♂	14								2	3	7	2		22.64	23
A. leilae	♀	4		1	3										15.75	16
	♂	2			2										16	—
A. myriamae	♀	4		2	2										15.5	—
A. tolimana	♂	2									1	1			22.5	—
	♀	2								1	1				21.5	—

with two small basal teeth, one median pronounced, one subdistal slightly shorter than the median, and one distal tooth. Internally with two strong teeth, one basal and one median, and one distal tooth that is larger than its external counterpart. Fixed finger externally with one basal and one median tooth mounted onto a bicuspid, one subdistal, and one distal tooth. Internally with only one tooth located slightly basal in respect to the external subdistal.

Coxosternal region: Sternum subtriangular, with a deep median depression and two anterolateral furrows; all the components of this region smooth, with few sparse setae; coxapophyses I–II with dense pilosity anteriorly.

Genital operculum and pectines: Genital operculum divided longitudinally; pectinal basal piece longer than wide; pectines long, surpassing the lateral margins of sternite III; count of pieces on the pectines: basal lamellae 3:3, middle lamellae 9:9, teeth 20:21, fulcra absent.

Sternites: III–IV completely smooth; V–VI with sparse weak granulation; VII densely granulose and with incomplete, parallel and vestigial paramedian carinae, lateral carinae completely absent (Fig. 4); sternites III–VII with abundant setae; sternite V with subtriangular posterior median smooth area; spiracles oval elongate.

Tergites: With similar granulation to that of the carapace; axial carina only evident in the posterior half of tergites II–VI; vestigial dorsolateral carinae also present in these tergites, represented by two or three slightly larger granules; tergite VII tetracarinate (paired dorsolateral and lateral carinae, incomplete), a median elevation is present in the position of the axial carina.

Metasoma: With few long setae; segments I–III with ten carinae (paired ventral, ventrolateral, intermedian, dorsolateral and dorsal carinae); segment IV with six (ventral and intermedian carinae absent) (Fig. 5); segment V with five (axial, paired ventrolateral and dorsolateral carinae); ventrolateral and intermedian carinae converge distally in segments I–II; ventral and ventrolateral carinae are connected anteriorly by a transverse row of granules in segments II–III; intermedian carinae on segment III are only present anteriorly; all carinae serrulose; intercarinal spaces with abundant weak granulation. Telson almost completely smooth, except for some granules located on the position of the axial carina; subaculear tubercle strong and spine-like; aculeus long and curved.

Pedipalps: With very fine granulation throughout; femur with five longitudinal carinae (dorsoexternal, dorsointernal, ventroexternal, ventrointernal and internal median carinae), with sparse weak rounded granules dorsally and internally; patella without distinct carinae but with few granules on the position of the dorsointernal and ventrointernal carinae; chela acarinate; fixed finger with six almost linear rows of granules (including the short apical row), the basal the longest; movable finger with seven rows. Trichobothriotaxy type A, femur with β configuration (Vachon 1973, 1975) (Figs. 6–11).

Legs: Tibia, basitarsus and telotarsus with numerous ventral setae; tibial spur present in legs III–IV; prolateral pedal spur single in legs I–II, bifid in legs III–IV; retrolateral pedal spur present in all the legs.

Measurements (mm).—Total L (excluding telson) 18.25; carapace L 2.46; carapace anterior W 1.51; carapace posterior W 2.28; interocular distance 0.15; ocular diameter 0.24. Mesosoma L 5.09. Metasoma L (including telson) 13.82: segments: I L/W/D 1.40/1.59/1.38; II L/W/D 1.59/1.47/1.38; III L/W/D 1.74/1.44/1.40; IV L/W/D 2.29/1.42/1.46; V L/W/D 3.68/1.54/1.36. Telson L 3.12; vesicle W/D 0.72/0.71. Pedipalps: total L 8.29; femur L/W 2.27/0.58; patella L/W 2.74/0.74; chela L/W/D 3.28/0.55/0.54; movable finger L 2.55; palm L 0.85.

←

carapace (only granulation of the ocular carinae is included); 4. Sternite VII; 5. Ventral view of metasomal segment IV; 6–11. Distribution of the trichobothria (illustrated from the right pedipalp); 6. Femur, dorsoexternal view; 7. Femur, internal view; 8. Patella, dorsointernal view; 9. Patella, external view; 10. Chela, external view; 11. Chela, ventral view. Abbreviations: PLC = paramedian longitudinal carina; VLC = ventrolateral carina; DLC = dorsolateral carina. Scale bars = 0.5 mm.

Table 2.—States for some taxonomically useful characters in all species of Colombian *Ananteris*. SAMC = Shape of the anterior margin of the carapace; TOC = Texture of the ocular carinae; RP $v_1 - v_2$ = Relative position of v_1 and v_2 trichobothria; RP Ext. – Dor. = Relative position of the external and dorsal trichobothria on pedipalp fixed finger (beginning from the base; "/" symbol indicates trichobothria at the same level); C St. VII = Carination of sternite VII; MCF = Metasomal carinal formula (* indicates that the intermedian carinae on segment III are vestigial and only present anteriorly). Data for *A. tolimana* are based on Teruel & García (2007).

Species	SAMC	TOC	RP $v_1 - v_2$	RP Ext. – Dor.	C St. VII	MCF
A. arcadioi	With anteromedian eminence	Granulose	Unaligned axially	*eb:esb:est/db:et:dt*	Paramedian present	10:10:10:6:5*
A. columbiana	With anteromedian eminence to slightly bi-concave	Granulose	Aligned axially	*eb:esb:db:est:et:dt*	Paramedian present	10:10:10:8:5*
A. dorae	Slightly concave	Granulose	Unaligned axially	*eb:esb:db:est:et:dt*	Acarinate	10:10:10:6:3
A. ehrlichi	Slightly concave	Granulose	Aligned axially	*eb:esb:est/db:et:dt*	Paramedian present	10:10:8:8:5
A. gorgonae	Slightly concave	Smooth	Aligned axially	*eb:esb:est/db:et:dt*	Paramedian present	10:10:10:8:5*
A. leilae	Slightly concave	Granulose	Aligned axially	*eb:esb:db:est:et:dt*	Paramedian present	10:10:8:8:5
A. myriamae	With anteromedian eminence	Granulose	Unaligned axially	*eb:esb:est/db:et:dt*	Paramedian present	10:10:10:6:5
A. tolimana	Slightly concave (see Teruel & García 2007: fig. 2a)	Granulose (see Teruel & García 2007: fig. 2a)	—	*...est/db...*	Paramedian present	10:10:10:8:5*

Female.—Unknown.

Distribution.—This species is known only from the type locality: Altamira, Puerto Gaitán, Meta Department (Fig. 1). It inhabits the Llanos ecoregion, which extends from the foothills of the Eastern Andes of Colombia through almost the entire course of the Orinoco River. It has a typical savanna climate, with wet and dry season and high temperatures all over the year. Besides the savanna areas, this ecoregion gathers a variety of forests in which most of its biodiversity is found (National Geographic Society 2001).

Affinities with other Colombian species.—*Ananteris arcadioi* is most similar to *A. myriamae*, with which it shares the anterior margin of the carapace with a well developed median eminence (Fig. 3; Botero-Trujillo 2007:fig. 6), the carinal formula of metasoma 10:10:10:6:5 with ventral and intermedian carinae absent on segment IV (Fig. 5), and that v_1 and v_2 trichobothria are not aligned axially (Fig. 11; Botero-Trujillo 2007:fig. 13). *Ananteris arcadioi* can be readily distinguished by the greater number of pectinal teeth (20–21), the low degree of reticulation on dorsal surface of chelicerae (Fig. 2), the intermedian carinae on metasomal segment III that are only present anteriorly, and the vestigial paramedian carinae of sternite VII that are parallel and formed by many granules (Fig. 4). In contrast, in *A. myriamae* the pectines have 15–16 teeth, the chelicerae are densely reticulated (Botero-Trujillo 2007: fig. 3), intermedian carinae are complete on metasomal segment III; and the vestigial paramedian carinae of sternite VII are not parallel (being separated from each other by a greater distance anteriorly than posteriorly) and are formed by two to four granules.

Ananteris dorae sp. nov.
Figs. 1, 12–21; Tables 1, 2

Type material.—*Holotype:* COLOMBIA: *Nariño Department*: adult female, Reserva Natural La Planada, permanent plot, 01°15′N, 78°15′W, 1885 m elev., pitfall, 2–4 May 2001, G. Oliva, M. 2369 (IAvH-E 100763).

Etymology.—Patronym dedicated to the memory of Dora Elizabeth Mendoza. It celebrates the lives of Dora and her family, who filled each other with support, encouragement, and inspiration.

Diagnosis (based on female only).—*Ananteris dorae* differs from all other species of the genus due to its unique metasomal carinal formula 10:10:10:6:3, with ventral and intermedian carinae absent on segment IV (Fig. 14) and ventrolateral carinae absent on segment V (Fig. 15). Other interesting and useful characters of the new species are: v_1 and v_2 trichobothria are not aligned axially but v_2 is located on an external position in relation to v_1 (Fig. 21); *est* and *et* trichobothria are located between *db* and *dt* on pedipalp fixed finger, and *esb* is basal to *db* (Fig. 20); the anterior margin of the carapace is weakly, evenly concave and lacking median eminence (Fig. 12); the dorsal surface of chelicerae exhibits a complete and very reticulated pattern; pectines have 13:13 teeth; sternite VII lacks any vestige of paramedian carinae (Fig. 13); metasomal segments present abundant and strong granulation, especially on segment V where the carinae are difficult to distinguish from the remaining granules of the tegument (Figs. 14, 15); and metasomal carinae are formed by unconnected granules (except for dorsolateral and dorsal carinae).

Description based on female holotype (IAvH-E 100763).—*Coloration:* General coloration dark brown over almost the entire body and appendages. Carapace predominantly dark brown with some lighter spots and bands; anterior and posterior margins dark brown; arising posterior to the lateral eyes there are two thin and almost straight light-brown lines, each directed toward the midline that do not reach it but end behind and beside the median ocular tubercle; median ocular tubercle black. Chelicerae dark brown, hand with a densely reticulated pattern in dorsal view; fixed and movable fingers almost black, teeth yellowish. Coxosternal region light brown; genital operculum, pectinal basal piece, pectines and sternites III–VI completely dark yellow; sternite VII brownish laterally;

sternite V with a much redueed posterior median hyaline area, a narrow transverse. Tergites predominantly dark brown; each side of tergites II–VI with two transverse yellow lines converging near the midline, arrow-like; tergite VII predominantly dark brown. Metasoma predominantly dark brown to reddish; dorsal intercarinal spaces of segments I–IV with a median dark brown design that is wider anteriorly, triangle-like in segments I–III; segments I–V with some dark red regions on all surfaces. Telson reddish, lighter than segment V, with inconspicuous brownish spots ventroexternally; aculeus reddish, lighter basally; subaculear tubercle brownish. Pedipalps predominantly dark brown; femur and patella with few regions slightly lighter externally and ventrally, insertion of all the trichobothria yellow in both segments; hand completely yellow; fixed and movable fingers dark brown, yellowish basally. Legs predominantly dark brown, except for the telotarsus that is completely yellow.

Carapace: With very fine granulation throughout, and densely covered with greater but weak rounded granules especially in the dark brown areas; lateral margins not parallel; anterior margin weakly, evenly concave and lacking median eminence (Fig. 12); ocular carinae evident, others inconspicuous; a median depression anterior to the ocular tubercle and a posterior median longitudinal furrow are evident; median ocular tubercle low, located in the posterior half of the anterior third of the carapace, with dense thin granulation and few greater granules in the ocular carinae; lateral ocular tubercles each with four ocelli, the posterior-most is very reduced and unaligned with the remaining three pairs (Fig. 12).

Chelicerae: With abundant fine white setae on the internal and ventral surfaces; cheliceral dentition characteristic of the family Buthidae (Vachon 1963). Movable finger externally with two small basal teeth, one median pronounced, one subdistal slightly shorter than the median, and one distal tooth. Internally with two strong and pronounced teeth, one basal and one median, and one distal tooth that is larger than its external counterpart. Fixed finger externally with one basal and one median tooth mounted onto a bicuspid, one subdistal, and one distal tooth. Internally with only one tooth located slightly basal in respect to the external subdistal.

Coxosternal region: Sternum subtriangular, with a deep median depression and two anterolateral furrows; all the components of this region smooth, with abundant setae; coxapophyses I–II with dense pilosity anteriorly.

Genital operculum and pectines: Genital operculum divided longitudinally; pectinal basal piece wider than long; pectines densely hirsute, surpassing the lateral margins of sternite III; count of pieces on the pectines: basal lamellae 3:3, middle lamellae 7:7, teeth 13:13, fulcra absent.

Sternites: III–IV completely smooth; V–VI with few weak granulations on the posterior border; VII densely granulose and without any vestige of paramedian or lateral carinae (Fig. 13); sternite IV bilobate posteriorly; sternites III–IV, VI–VII with very few setae; sternite V densely hirsute medially, with a much reduced posterior median smooth area, a narrow transverse; spiracles linear.

Tergites: With similar granulation to that of the carapace; axial carina only evident in the posterior half of tergites III–VI; dorsolateral and lateral carinae completely absent in tergites I–VI; tergite VII tetracarinate (paired dorsolateral and lateral carinae, incomplete), a median elevation is present in the position of the axial carina.

Metasoma: With few setae; segments I–III with ten carinae (paired ventral, ventrolateral, intermedian, dorsolateral, and dorsal carinae); segment IV with six (ventral and intermedian carinae absent) (Fig. 14); segment V with three (axial, paired dorsolateral carinae) (Fig. 15); ventrolateral and intermedian carinae converge distally in segments I–II; ventral carinae are not parallel in segment I but arranged into S-shape, separated from each other by a greater distance anteriorly than posteriorly; ventral carinae are connected to each other and to ventrolateral carinae by a transverse row of granules in segments II–III; all carinae granulose, formed by unconnected granules (except for dorsolateral and dorsal carinae in segments I–IV whose granules are very close together); intercarinal spaces with abundant strong granulation (Figs. 14, 15). Telson bulbous, densely granulose ventrally and externally, smooth dorsally, with vestigial axial and ventrolateral carinae; subaculear tubercle strong and spine-like; aculeus short and curved.

Pedipalps: With very fine granulation throughout; femur with five vestigial longitudinal carinae (dorsoexternal, dorsointernal, ventroexternal, ventrointernal and internal median carinae); patella without distinct carinae but with few greater granules on the position of the dorsointernal and ventrointernal carinae; chela acarinate; fixed finger with six almost linear rows of granules (including the short apical row), the basal the longest; movable finger with seven rows. Trichobothriotaxy type A, femur with β configuration (Vachon 1973, 1975) (Figs. 16–21).

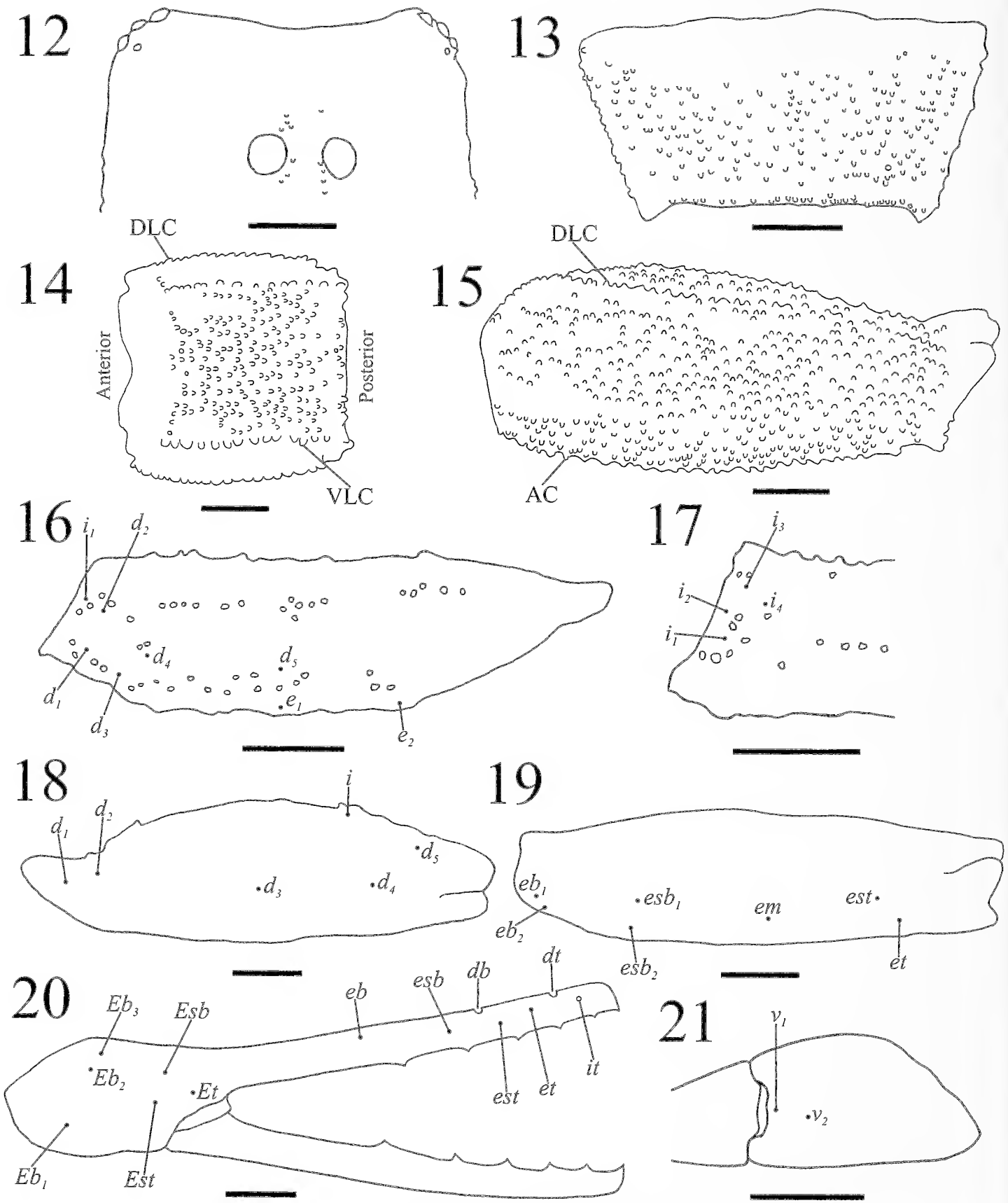
Legs: Basitarsus and telotarsus with numerous ventral setae; tibial spur present in legs III–IV; prolateral pedal spur single in legs I–II, bifid in legs III–IV; retrolateral pedal spur present in all the legs; tarsal claws long and curved, exceeding the depth of the telotarsus.

Measurements (mm).—Total L (excluding telson) 16.20; carapace L 2.20; carapace anterior W 1.58; carapace posterior W 2.46; interocular distance 0.20; ocular diameter 0.20. Mesosoma L 5.27. Metasoma L (including telson) 11.65: segments: I L/W/D 1.16/1.46/1.09; II L/W/D 1.28/1.42/1.10; III L/W/D 1.37/1.33/1.20; IV L/W/D 1.89/1.35/1.32; V L/W/D 3.03/1.39/1.28. Telson L 2.92; vesicle W/D 1.06/1.00. Pedipalps: total L 8.29; femur L/W 2.21/0.60; patella L/W 2.68/0.79; chela L/W/D 3.40/0.53/0.58; movable finger L 2.56; palm L 0.86.

Male.—Unknown.

Distribution.—This species is known only from the type locality: Reserva Natural La Planada, Nariño Department (Fig. 1). It inhabits the Northwestern Andean Montane Forests ecoregion, which is among the most diverse ecoregions on the planet. Due to Andean topography and pronounced glacial period of isolation, the ecosystems present in this region exhibit a diverse array of distinctive communities with unusual high levels of species endemism (National Geographic Society 2001).

Affinities with other Colombian species.—*Ananteris dorae* is most similar to *A. myriamae* and *A. arcadioi*, with which it shares the presence of six carinae in metasomal segment IV with ventral and intermedian carinae absent (Figs. 5, 14), and



Figures 12–21.—*Ananteris dorae* sp. nov., female holotype (IAvH-E 100763): 12. Anterior margin of the carapace (only granulation of the ocular carinae is included); 13. Sternite VII; 14. Ventral view of metasomal segment IV; 15. Lateral view of metasomal segment V; 16–21. Distribution of the trichobothria (illustrated from the right pedipalp); 16. Femur, dorsoexternal view; 17. Femur, internal view; 18. Patella,

that v_1 and v_2 trichobothria are not aligned axially (Figs. 11, 21; Botero-Trujillo 2007:fig. 13). *Anauteris dorae* can be readily distinguished from both species since in the former the anterior margin of the carapace is weakly, evenly concave and lacking median eminence (Fig. 12), sternite VII lacks any vestige of paramedian carinae (Fig. 13), metasomal segment V is tricarinate with ventrolateral carinae absent (Fig. 15), metasomal segments have abundant and strong granulation, especially on segment V where the carinae are difficult to distinguish from the remaining granules of the tegument (Figs. 14, 15), metasomal carinae are formed by unconnected granules (except for dorsolateral and dorsal carinae), the pectinal teeth number is lower (13:13), and *db* trichobothrium is considerably basal to *est* on pedipalp fixed finger (Fig. 20). In contrast, in *A. myriamae* and *A. arcadioi* the carapace has a well developed anteromedian eminence (Fig. 3; Botero-Trujillo 2007:fig. 6), sternite VII bears vestigial paramedian carinae (Fig. 4), metasomal segment V is pentacarinate, the granulation of metasomal segments is less abundant and weaker, metasomal carinae are formed by connected granules, the pectinal teeth number is greater (*A. myriamae*: female 15–16; *A. arcadioi*: male 20–21), and *db* is located beside *est* (Figs. 10; Botero-Trujillo 2007:fig. 12).

COMMENTS ON THE TAXONOMY OF COLOMBIAN *ANANTERIS*

The examination of several specimens of this genus belonging to various species—and others that do not fit into any of the known species and thus remain under study—from many Colombian localities, highlighted that the genus *Ananteris* provides few taxonomically useful characters. The widely used pectinal teeth number and coloration pattern, despite being useful, ideally should not be used alone to identify species because specimens belonging to different species may overlap in the number of teeth (Table 1) and in general color patterns. In review of the morphological characters used to diagnose species within the genus *Ananteris* the usefulness of some was confirmed and others never previously used appeared to be useful, whereas others exhibited intraspecific variability and therefore their use to define species should be avoided. Below, these characters are organized in three sections depending on their usefulness. Authors are strongly encouraged to include in their contributions to the genus *Anauteris* detailed descriptions and/or illustrations of these features, in order to better ascertain their taxonomic value.

Taxonomically useful characters (variable among species, easily defined).—*Shape of the anterior margin of the carapace:* This has been only previously used to assist the diagnosis of a species of *Ananteris* by Botero-Trujillo (2007). Two states have been identified for this character: *i)* straight or with a slight concavity; *ii)* not straight, with anteromedian eminence whose strength appears to also be useful. Even though some individual variations in the strength of the pronouncement have been observed in *A. columbiana*, it is the same among the two known specimens of *A. myriamae* and is invariable in a different species that remains under study of which several specimens are available.

Texture of the ocular carinae: This has never been used previously in *Anauteris*, but is herein used to distinguish *A. gorgonae* from all other Colombian species (Table 2). Two states have been identified for this character: *i)* with granules in the interocular region similar to granules of the carapace; *ii)* smooth.

Relative position of "v_1" and "v_2" trichobothria on pedipalp chela: This has been only previously used by Botero-Trujillo (2007). Two states have been identified for this character: *i)* these are arranged linearly parallel to the external surface of the pedipalp chela (aligned axially); *ii)* the resulting line is not parallel to the external surface, with v_2 located on an external position in relation to v_1 (unaligned axially). It is important to note that, even though Lourenço's (1999a:fig. 2) illustration of the arrangement of these trichobothria in the female holotype of *A. leilae* shows these unaligned, examination of this scorpion (ICN-MHN-As-110) revealed that these are actually aligned axially, as in the other two specimens available of this species.

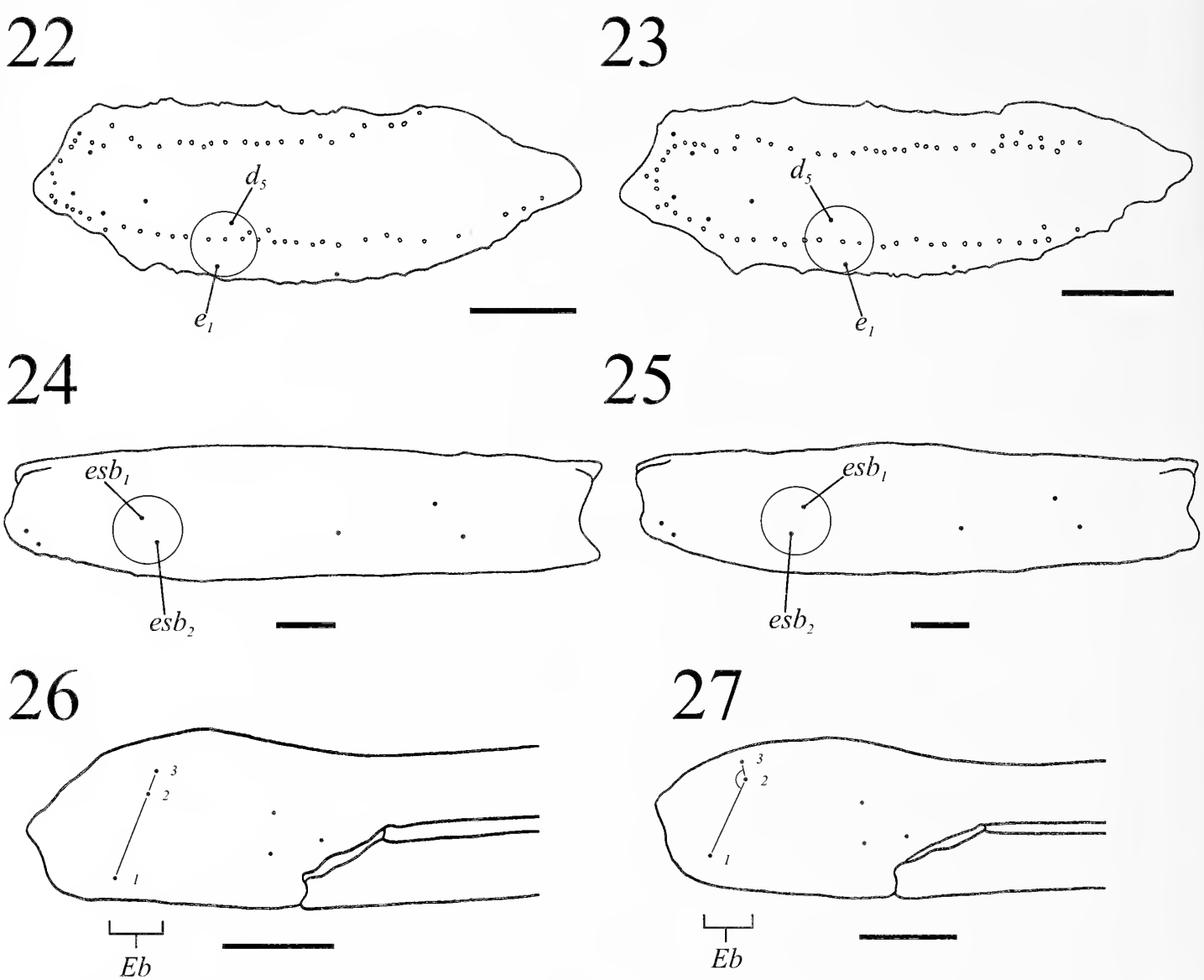
Position of "db" trichobothrium with respect to "est" on pedipalp fixed finger: This has been mentioned to be useful in several studies (Lourenço 1982, 1984, 1999b, 2002a, 2002b; González-Sponga 2006; Teruel & García 2007). Two states have been identified for this character: *i) db* beside *est* or nearly so; *ii) db* basal to *est*. It is important to note that in a few specimens, particularly *A. columbiana*, the position of *db* with respect to *est* presents slight differences between both chelae, which does not necessitate the need to abandon the system. In addition to the relative position of these two trichobothria, it is noteworthy that several different arrangements of the dorsal and external trichobothria on pedipalp fixed finger have been identified in the entire genus (i.e., *eb*:*esb*:*est*/*db*:*et*:*dt*, *eb*:*esb*:*db*:*est*:*et*:*dt*, *eb*:*esb*:*est*:*db*:*et*:*dt*, *eb*:*esb*:*db*:*est*:*dt*/*et*, *eb*:*db*:*esb*:*est*:*db*:*et*, *eb*:*db*:*esb*:*est*:*et*:*dt*, beginning from the basal most and the "/" symbol indicating trichobothria at the same level), thus appearing to be a very useful taxonomic character.

Carination of sternite VII: This has never been used previously in *Anauteris*, but is herein used to assist the diagnosis of *A. dorae*. Two states have been identified for this character: *i)* without any vestige of paramedian carinae; *ii)* with vestiges of such carinae, whose length and arrangement appears to also be useful.

Metasomal carinal formula: This refers to the number of carinae that are present on the metasomal segments. It is frequently expressed in the way of Arabic numerals separated by a colon, beginning from segment I. The number of carinae on metasomal segments has been widely used to distinguish species (Lourenço 1982, 2002b, 2004a; Rojas-Runjaic 2005; González-Sponga 1972, 1980, 1996, 2006; Kovařík 2006; Botero-Trujillo 2007), and several different combinations have been observed in the entire genus (i.e., 10:10:10:10:5,

←

dorsointernal view; 19. Patella, external view; 20. Chela, external view; 21. Chela, ventral view. Abbreviations: VLC = ventrolateral carina; DLC = dorsolateral carina; AC = axial carina. Scale bars = 0.5 mm.



Figures 22–27.—Characters that are variable within species of *Ananteris*. Some segments are inverted for easier comparisons. 22, 23. Position of femoral "d_5" trichobothrium with respect to "e_1"; example from *A. columbiana*: 22. Right femur of an adult female (ICN-MHN-As-121); 23. Left femur of an adult female (ICN-MHN-As-111). 24, 25. Position of patellar "esb_1" with respect to "esb_2"; example from *A. elirlichi*: 24. Right patella of an adult female (ICN-MHN-As-361); 25. Left patella of an adult female (ICN-MHN-As-342). 26, 27. Position of "Eb_1", "Eb_2" and "Eb_3" on chela; example from *A. columbiana*: 26. Right chela of a female (ICN-MHN-As-111); 27. Right chela of a female (ICN-MHN-As-121). Scale bars = 0.5 mm.

10:10:10:6:2, 10:10:10:6:3, 10:10:10:6:5, 10:10:10:8:5, 10:10:8:8:5, 10:8:8:8:5 among others). The carination of segments IV–V appears the most useful for the identification of Colombian species. Two states have been identified in segment IV: *i)* eight carinae, with only intermedian absent; *ii)* six carinae, with ventral and intermedian absent. Two states have been identified in segment V: *i)* five carinae; *ii)* three carinae, with ventrolateral absent. Caution should be taken in the assignment of state to segment III, since the intermedian carinae may be weakly developed and only present anteriorly. In such a case, it is recommended that these be included in the formula but its condition indicated as in Table 2, since the length of this particular pair of carinae has been shown to also be useful.

Taxonomic characters of restricted usefulness (variable among species, difficult to define).—These characters are useful to diagnose species provided that additional characters are considered. *Cheliceral reticulation*: the degree and pattern of reticulation on the dorsal surface of the chelicerae have been observed to be almost always constant within species, virtually invariable among sexes and maturity, thus having been mentioned as taxonomically useful in many studies (Lourenço 1982, 1987, 1997, 1999c, 2001, 2002a, 2002b, 2003, 2004b; Kovařík 2006; Teruel & García 2007). Only very few specimens with slight variations have been found, which does not render this character useless.

Pectinal teeth number: Perhaps one of the most frequently used characters to assist the diagnosis of scorpion species. In *Ananteris* it has been widely used previously (Lourenço 1981, 1982, 1999a, 2002a, 2002b; Lourenço & Flórez 1989; González-Sponga 2006; Kovařík 2006; Botero-Trujillo 2007;

Teruel & García 2007). This character should not be used alone since the ranges overlap among many species and it is sex-dependent in many cases (Table 1).

Shape of the posterior median hyaline and smooth area on sternite V: This area has only been previously used to assist the diagnosis of a species of *Ananteris* by Teruel & García (2007). Even though it has been observed that the shape of this structure is almost invariable within species, it is not easy to define character states since it would depend on each author's perceptions. In addition, it has been observed that the degree of development of this structure may be sex-dependent [as noted by Teruel & Garcia (2007) for *A. tolimana*] and is absent or very difficult to identify in juveniles.

Pilosity of the sternites and metasomal segments (size and density); granulation of metasomal segments (strength and density): These have never been used previously in *Ananteris*, except for the later that is herein used to assist the diagnosis of *A. dorae*. Even though it has been observed that the size and density of setae on the sternites, and the strength and density of the granulation on metasomal segments may vary depending on the species, it is not recommended that these be used alone to define species given that they present gradual variation, thus being difficult to define character states.

Taxonomic characters that are not useful (variable within species).—*Position of femoral "d_5" trichobothrium with respect to "e_1"; of patellar "esb_1" to "esb_2"; and of "Eb_1", "Eb_2" and "Eb_3" to each other on chela:* Of these, only the relative position of femoral d_5 and e_1 trichobothria has been used to distinguish species of *Ananteris* (Lourenço 1984, 2002a, 2002b). Even though these were first thought to be useful for the identification of Colombian species when differences were observed among them, examination of as many specimens as possible revealed that, although one or another arrangement may tend to be more common on each species, the relative position of these trichobothria is variable (Figs. 22–27).

KEY FOR THE IDENTIFICATION OF COLOMBIAN *ANANTERIS*

Users of this key should be aware that the genus *Ananteris* has recently shown a notorious increase in the number of known species; thus, it is likely that many other species that have not yet been described may fit in the key, leading to erroneous conclusions on their taxonomic identity. Besides this, many species of *Ananteris* are based upon few taxonomic characters, making their identification even more difficult. Therefore, it is strongly recommended that any conclusion be tested *a posteriori* with the aid of the original descriptions and supported by the information on the geographic distribution of each species since most have exhibited restricted distribution patterns.

1. Metasomal segment IV with six complete carinae (paired dorsal, dorsolateral and ventrolateral carinae) and ventral and intermedian carinae absent (Figs. 5, 14); v_1 and v_2 trichobothria unaligned axially, with v_2 located on an external position in relation to v_1 (Figs. 11, 21; Botero-Trujillo 2007:fig. 13) 2
   Metasomal segment IV with eight complete carinae (only intermedian carinae absent); v_1 and v_2 trichobothria aligned axially 4
2. Metasomal carinal formula10:10:10:6:3 with all carinae complete and ventrolateral carinae absent on segment V (Fig. 15); sternite VII without paramedian carinae (Fig. 13); carapace slightly concave anteriorly and lacking anteromedian eminence (Fig. 12) . . . . . *Ananteris dorae*
   Metasomal carinal formula 10:10:10:6:5, with intermedian carinae on segment III either complete or only present anteriorly; sternite VII with incomplete paramedian carinae (Fig. 4); carapace with anteromedian eminence (Fig. 3; Botero-Trujillo 2007: fig. 6) 3
3. Intermedian carinae on metasomal segment III only present anteriorly; chelicerae with an incomplete reticular pattern on dorsal surface (Fig. 2); paramedian carinae on sternite VII parallel and formed by many granules (Fig. 4) . . . . . *Ananteris arcadioi*
   Intermedian carinae on metasomal segment III complete; chelicerae with a complete reticular pattern on dorsal surface (Botero-Trujillo 2007:fig. 3); paramedian carinae on sternite VII separated by a greater distance anteriorly than posteriorly and formed by no more than four granules . . . . . *Ananteris myriamae*
4. Metasomal carinal formula 10:10:10:8:5 with intermedian carinae on segment III only present anteriorly 5
   Metasomal carinal formula 10:10:8:8:5 with intermedian carinae completely absent on segment III 7
5. Ocular carinae smooth; male pectines with 21–24 teeth . . . . . *Ananteris gorgonae*
   Ocular carinae granulose; male pectines with 16–18 or 22–23 teeth 6
6. Trichobothrium *est* located beside *db* on pedipalp fixed finger (as in Fig. 10); pectines with 22–23 teeth in males, 21–22 in females; sternites III–V with conspicuous brown regions (Teruel & García 2007: fig. 2c, 2b) . . . . . *Ananteris tolimana*
   Trichobothria *est* and *et* located between *db* and *dt* on pedipalp fixed finger (as in Fig. 20); pectines with 16–18 teeth in males, 15–19 in females; sternites III–V completely yellow or, if any spots, then these are minute and inconspicuous *Ananteris columbiana*
7. Trichobothria *est* and *et* located between *db* and *dt* on pedipalp fixed finger (as in Fig. 20); female pectines with 15–16 teeth; pedipalp hand completely yellow . . . . . *Ananteris leilae*
   Trichobothrium *est* slightly basal to *db* or beside it on pedipalp fixed finger; female pectines with 21–23 teeth; pedipalp hand with conspicuous brown areas in all surfaces . . . . . *Ananteris ehrlichi*

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Alternative predatory tactics in a juvenile jumping spider

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Abstract. The hunting behavior of juvenile *Yllenus arenarius* Menge 1868 in their first week after leaving sub-sand nests was studied. The spiders were tested with prey that can effeetively escape (Homoptera) and prey that are not capable of efficient escape (Thysanoptera and larvae of Lepidoptera) in order to assess the complexity of young spiders' hunting tacties. Numerous differences were found in the mode of catching the prey, which indicate that the spiders possess a conditional hunting strategy. The strategy is expressed in: direction of approach, speed of approach, distance of attack and other prey-specific behaviors. The results strongly suggest the pre-programmed background of both the observed behaviors and sensitivity towards certain prey characteristics that enabled prey identifieation.

Keywords: Predatory behavior, conditional strategy, Salticidae, *Yllenus*

The studies of salticid behavior reveal examples of extraordinary cognitive abilities of these small invertebrates with very small neural systems. A well-studied example includes spiders from the genus *Portia* Karsch 1878, these are gradually becoming models in the study of invertebrate cognition (Wilcox & Jackson 1998; Harland & Jackson 2004). They are able to invade alien webs, generating variable aggressive-mimicry signals (Jackson & Wilcox 1993a), or – using opportunistic smokescreen behaviors – approach the spider host without being noticed (Wilcox et al. 1996). If *Portia* cannot approach a web spider directly, it performs a detour (Jackson & Wilcox 1993b), and can also choose between two alternative routes selecting the one that leads to prey (Tarsitano & Jackson 1997).

One key to the majority of complex salticid behaviors is their extraordinary eyesight, which allows preeise discrimination between different prey types and prey characteristics (Harland & Jaekson 2002). Jumping spiders exploit subtle signals from their prey and the environment. In addition, they tune their hunting tactics in various conditions, e.g., when they approach dangerous invertebrates (Harland & Jackson 2002), when the invertebrates are facing them (Li et al. 2003), when they are highly visible to the prey (Bear & Hasson 1997), when the hunted foe's ability to defend is impaired (Wilcox et al. 1996; Li & Jackson 2003), when it is impossible to reach the prey directly (Jackson & Wileox 1993b; Tarsitano & Jackson 1997) or when the prey ean easily escape (Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2007).

Studies of hunting behavior are dominated by research on adult individuals with juveniles highly underrepresented. This is primarily because of certain impediments (juveniles are smaller, and it is more difficult to find and identify them to species, sex, or age). However, the studies of juvenile predation provide an opportunity to observe highly food-constrained animals at the stage when the main maximized traits are effective prey capture and predator avoidance, while other behaviors, e.g., reproductive activities, do not interfere with the former. Research on naive individuals allows us to analyze pre-programmed behavior and learning processes (e.g., Simonds & Plowright 2004).

There are hundreds of studies on the predatory behavior of adult jumping spiders (reviewed in Jaekson & Pollard 1996), but only a few dealing with those of inexperienced individuals (Forster 1977; Edwards & Jackson 1994). The study on *Phidippus regius* C.L. Koch 1846 (Edwards & Jackson 1994) revealed the innate and relatively eomplex character of basic hunting tactics. The authors pointed out the significantly different techniques used to capture flies and caterpillars by inexperienced individuals. They also stressed the importance of experience and maturity on hunting success. Recently it was found that in *Evarcha culicivora* (Wesolowska & Jackson 2003) prey-specific capture behaviors may be age dependent (Nelson et al. 2005).

The model used in our study was *Yllenus arenarius* Menge 1868 – a medium-sized jumping spider with an adult body length of about 7 mm. The cryptically-colored spiders inhabit sparsely vegetated dunes of Central and Eastern Europe (Proszynski 1986; Logunov & Marusik 2003), where they occupy the areas of bare sand between the grass. The spiders build nests made of silk and sand grains ca. 5 mm under dune surface, where they lay eggs, molt, hibernate and take shelter against night-active predators and periods of inclement weather (Bartos 2002a). Females lay on average 6 eggs in a special chamber within the nest. Juveniles hatch after about two weeks and stay together in the eommon chamber of the nests. After leaving nests they are about 1.1 mm and do not disperse for 1–2 days. At that time, they start hunting and build their own nests on a daily basis (Bartos 2002a, 2005). *Yllenus arenarius* is a polyphagous, sit-and-wait predator feeding on a wide range of insects and spiders that inhabit open sand or are blown by the wind onto the dune surface from neighboring habitats (Bartos 2004). Adult spiders were found to express a conditional hunting strategy expressed in jumping distance (Bartos 2002b), speed of approach, direction of approach, and other prey-specific behaviors (Bartos 2007).

We wished to determine whether the complex predatory strategy found in adults is also present in very young spiders. For the strategy to be functional, two conditions should be fulfilled. One is that even in young spiders there would need to be the ability to discriminate between variable prey items. These prey are diverse and are probably never seen in the same way – that is, they are of different species, age, size, coloration; and are seen from different angles and under different environmental conditions (e.g., light). Another condition is

Table 1.—Prey taxa used in the experiments.

Prey species	Order and family	Ability to escape	Body length (mm)
Psammotettix sp.	Homoptera, Cicadellidae	High	2
Thrips trehernei	Thysanoptera, Thripidae	Low	1
Chirothrips manicatus	Thysanoptera, Thripidae	Low	1
Pyralis farinalis	Lepidoptera, Pyralidae (larvae)	Low	2–4
Autographa gamma	Lepidoptera, Noctuidae (larvae)	Low	2–4

that the young spiders must possess tactics towards all the prey types with respect to the prey's position, size, speed of movement, etc. This study explores whether juvenile spiders in the first days after emergence from their sub-sand nests are able to: a) identify different prey types that vary in their escape potential, b) use the whole set of prey-specific hunting tactics reported from adults (Bartos 2007).

METHODS

Prey.—On the basis of a diet analysis carried out before the experiments (Bartos 2004) three taxa of common, natural prey were chosen from the insect orders: Homoptera, Thysanoptera, and larvae of Lepidoptera (Table 1). Prey items are markedly different according to many characteristics (e.g., shape, mode of movement, presence or absence of wings or antennae), but for a predator the most important feature is their ability to escape. The nymphs of Homoptera possess jumping legs, which enable effective escape, and were therefore regarded as prey of high escape ability. Thrips and caterpillars are unable to move quickly and were considered prey of low escape risk. Thrips were chosen as prey with characteristics that can be treated as intermediate between typical prey with high escape potential and low escape potential. They possess delicate, membranous wings, which, however, make effective escape almost impossible. Their elongated bodies often twist in motion make them similar to larvae, but they use thoracic legs to move. Each prey item was given to the spider of approximately similar size.

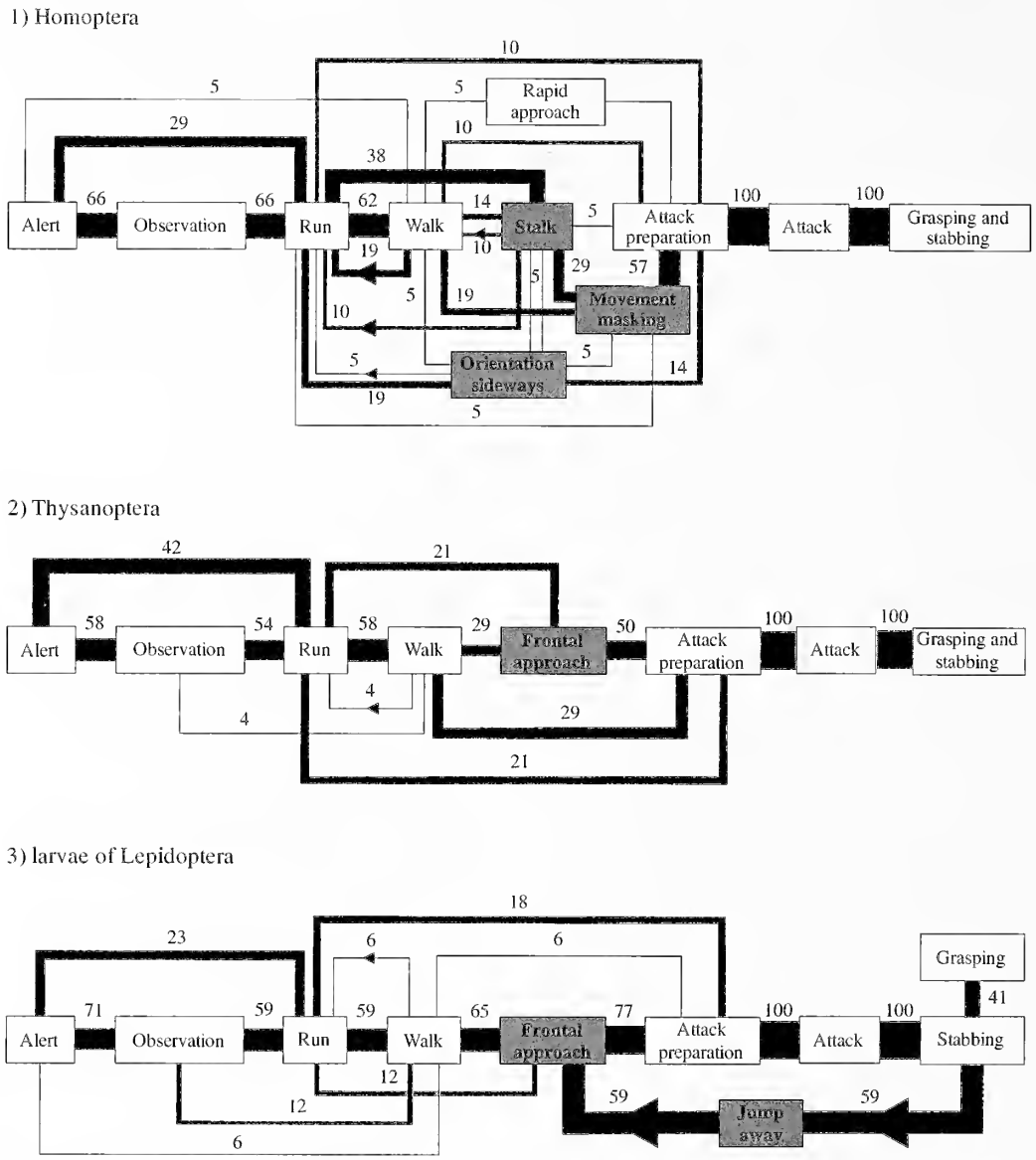
Homopterans and thrips were collected in the field by sweep-netting dune grass on the day of the experiment or the day before. They were brought to the lab and kept individually. Caterpillars were obtained from a laboratory culture. Each prey and a spider were chosen randomly for the experiments. In order to reduce mortality of the prey, inseets were stored in a refrigerator (at 5° C) and taken out 15 min before the experiment started.

Predators.—Spiders were collected from a dune in Central Poland (Kwilno, 51°59′N, 19°30′E). Young specimens were obtained directly from the field soon after they had emerged from their sub-sand nests. To estimate the date of emergence, the crucial phases of the spider's life cycle determined in earlier studies were used (Bartos 2005). In the period preceding the juveniles' emergence from their underground nests the dune surface was carefully searched. The search was carried out on a daily basis starting three weeks before the expected date of juveniles' appearance on the surface. Each day the sand surface was searched for four hours, which enabled checking about a quarter of the whole area inhabited by the studied population of *Y. arenarius*. When the first individual from the new cohort was found, the searching was intensified to collect all the newly hatched spiders from the area. The spiders were collected for seven days. Even though this method does not exclude the possibility that the spiderlings had prior experience with prey, such probability is low for the following reasons: a) the prey used in the tests (especially of the suitable size) were rare in the studied period, especially in the bare areas of the dune where spiderlings are found – only three out of about 200 juveniles were found with prey (a leafhopper) (Bartos unpubl. observ.); b) young spiders from the same nest were found close to each other (up to 1.5 m) for 1–2 days after hatching, which suggests that the tendency to disperse was limited in the period as was the tendency to demonstrate predatory behavior (Forster 1977).

The experiments were carried out the same day or the next day the spiders were collected in order to reduee the influences of rearing conditions on the spider's behavior (Carducci & Jakob 2000; Bartos unpubl. observ.). Before the experiments, spiders were kept individually in glass containers (10 cm height, 10 cm by 10 cm width) with a layer of dune sand on the bottom. Each spider was chosen randomly and used only once in the whole set of tests. The total number of spiders tested was almost 300, but only in c. 40% were hunting sequences observed. The experiments in which no hunting behavior was present (e.g., because the spider ignored the prey or the prey escaped before it was approached) have not been included in the data. The number of experiments in which the spider hunted the prey is given as n.

Experimental procedure.—Experiments were carried out within a white cardboard arena (15 cm height by 20 cm diameter) with a 1 cm-thick sand layer on the bottom. All the experiments were conducted between 09:00 hours and 16:00 hours (laboratory light regime, 12L:12D, lights coming on at 08:00 hours). Lighting was from a 100W PILA incandescent lamp bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena. Spiders were placed within the arena and, after one minute, a prey item was introduced about 8 cm from the spider. The prey was dropped approximately 30° to the left or right from the main eye's optical axis to allow the experimenter to record the moment when the predator oriented toward the prey. The prey item was left with the spider for 15 minutes. The hunting behavior was recorded with a camera placed above the arena.

Data analysis.—Movies with hunting sequences were analyzed, the behaviors observed, and the hunting success recorded. The complete sequences of hunting, namely those that started with the first dynamic behavior (run), and that ended with subduing the prey were used to draw flow diagrams (Figs. 1–3). If there were multiple attacks of a spider on the same prey, only the first hunting sequence was included. The percentage of individuals that expressed certain behaviors is indicated by the width of the line that leads to the behavior and by the number above the line. The numbers in some paths do not add up to 100%, due to rounding. The



Figures 1–3.—The flow diagrams of young *Y. arenarius* hunting three prey taxa. 1. Homoptera (n = 21); 2. Thysanoptera (n = 24); 3. larvae of Lepidoptera (n = 17). Transition frequencies are indicated by the percent numbers and by an appropriate line width. Grey boxes indicate prey-specific behaviors. The sequence should be read from left to right unless indicated by an arrow.

names of already reported components of salticid behavior are taken from a classic paper by Forster (1977). Behaviors specific for *Y. arenarius* adults are defined and discussed in Bartos (2007) and used here when appropriate

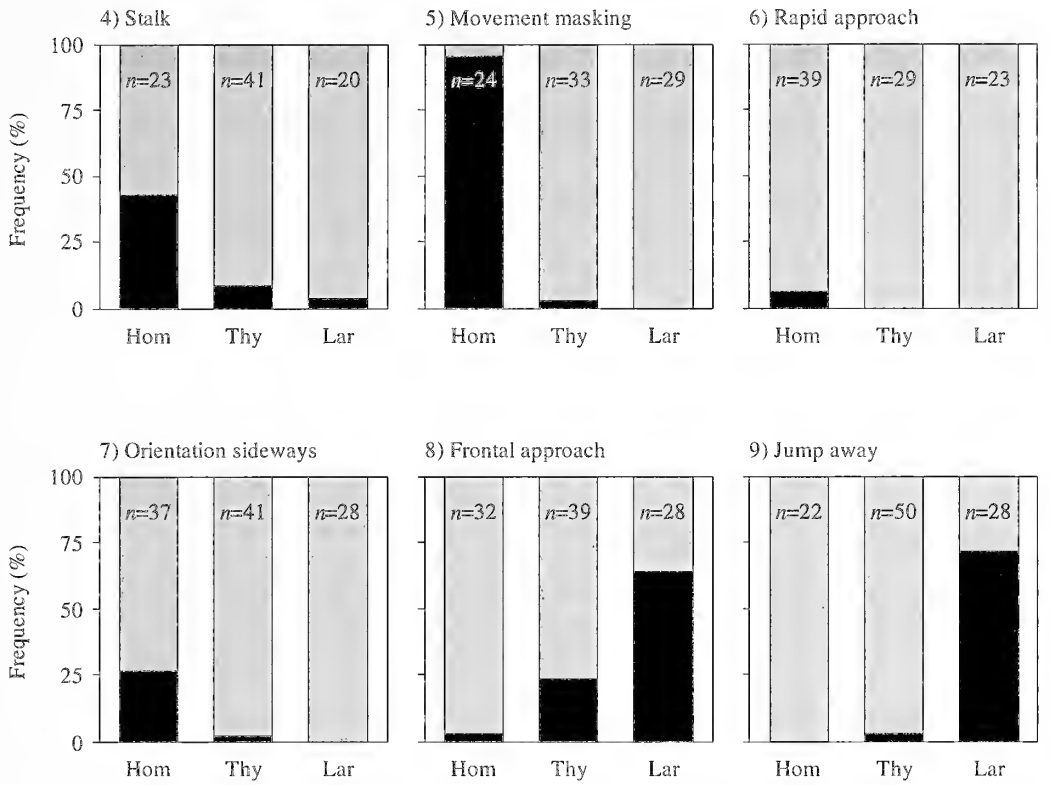
Abdomen length of spider was used to standardize the jumping distance to correct for body size and for the condition of different spiders in the same age (explanation in Bartos 2002b).

All statistical procedures followed those described by Zar (1984). To test the differences in frequency of behaviors, the Pearson's chi-squared test with Bonferroni adjustment was used (χ^2). To test differences in hunting distances the Kruskal-Wallis test was used (H^0).

RESULTS

Numerous differences were observed between episodes of catching prey with high escape potential (Homoptera) and low escape potential (Thysanoptera and larvae of Lepidoptera) (Figs. 1–9). Leafhoppers were approached in a more complex and variable way with many alternative phases of accelerating to *run* and decelerating to *walk*, *stalk* (very slow, choppy gait) or *movement masking* (approach only when the prey was moving) (Fig. 1). They were *stalked* more often than thrips and caterpillars (χ^2 = 17.1, df = 2, $P < 0.001$) (Fig. 4). The dissimilarity was even more clearly manifested in the *movement masking* (χ^2 = 74.1, df = 2, $P < 0.001$) (Fig. 5). Spiders approaching some leafhoppers *walked* or *ran* around the prey with the main eyes constantly focused on the target. Such movements, termed *orientation sideways*, were typical for hunting the prey (χ^2 = 17.1, df = 2, $P < 0.001$) (Fig. 7). Spiders performed *rapid approach* only when hunting leafhoppers (Figs. 1, 6). However, the behavior was very rare and there were no differences in the spiders' approach to different prey (χ^2 = 2.7, df = 2, $P > 0.05$).

The above pattern was uncommon in the corresponding phases of approach to thrips and caterpillars (Figs. 2, 3). These two prey types were typically approached at high speed



Figures 4–9.—The frequency of six prey-specific behaviors of young *Y. arenarius* hunting Homoptera (Hom), Thysanoptera (Thy) and larvae of Lepidoptera (Lar) by *Y. arenarius*. The behaviors are: 4. Stalk; 5. Movement masking; 6. Rapid approach; 7. Orientation sideways; 8. Frontal approach; 9. Jump away.

and without any apparent preventative measures. The caterpillars were the most commonly approached and attacked from the front side (Fig. 8), which was very rarely observed in the case of leafhoppers ($\chi^2 = 28.7$, $df = 2$, $P < 0.001$). Caterpillars were typically left for a period of time after venom injection. Such *jump away* was absent when hunting Homoptera and it was very rare when thrips were hunted ($\chi^2 = 58.3$, $df = 2$, $P < 0.001$) (Fig. 9).

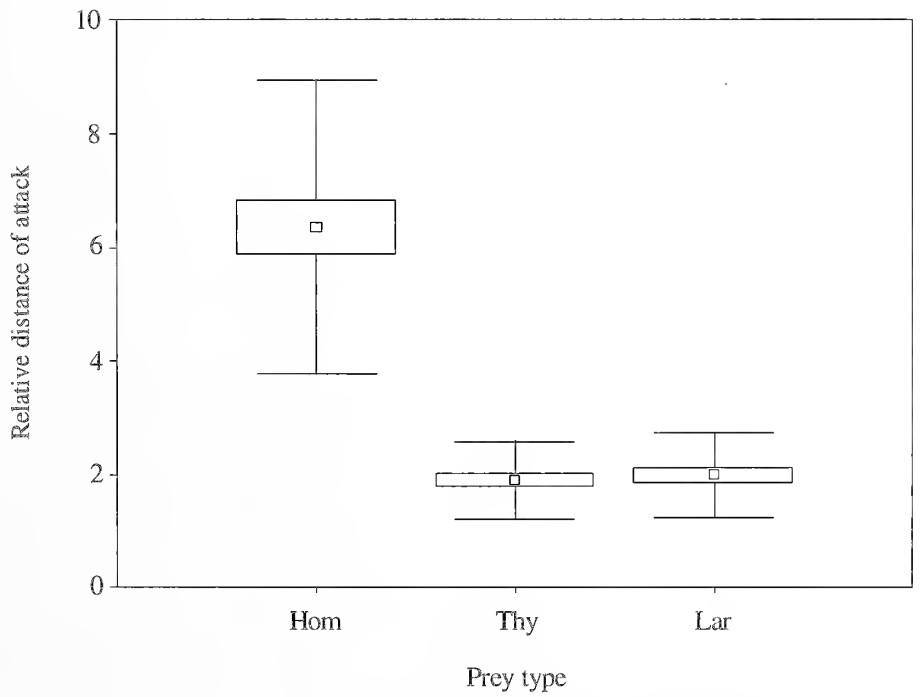


Figure 10.—Relative distance of attack (distance of attack/abdomen length) of young *Y. arenarius* hunting Homoptera (Hom) ($n = 29$), Thysanoptera (Thy) ($n = 25$) and larvae of Lepidoptera (Lar) ($n = 29$). Whiskers are SD, boxes are SE, central point is mean.

The modes of subduing prey were similar for hunting leafhoppers and thrips, but caterpillars were subdued differently (Figs. 1–3). Leafhoppers and thrips were first *grasped* and then *stabbed* without releasing (Figs. 1, 3). Caterpillars were *stabbed* and, in the majority of cases, left by means of *jump away* (Fig. 3). The wriggling larva was never abandoned, but it was constantly observed by the predator and after a while another strike was launched. After several attacks the prey was finally grasped. In the remaining episodes, spiders hunting larvae grasped the twisting prey and tried to subdue it (Fig. 3).

Significant differences were found in the jumping distance (Fig. 10). Homoptera were attacked from a longer distance than Thysanoptera and larvae of Lepidoptera – both were attacked in a similar way ($H^0 = 42.4$, $df = 2$, $P < 0.001$).

DISCUSSION

The hunting tactics of juvenile *Y. arenarius* soon after leaving sub-sand nests were relatively complex. The mode of approach was in many aspects similar to those of juvenile generalist salticids tested with analogous prey (Forster 1977; Edwards & Jackson 1994). The pattern of hunting all three prey types corresponded with the basic categories and subcategories summarized by Forster (1977, 1982) thus showing some universal hunting patterns of a juvenile, non-specialized salticid. All the tactics were similar to those of adult *Y. arenarius* tested with the same prey (Bartos 2007), which suggests that the basic patterns in the hunting strategy are not substantially modified with age. Even though the spiders' experience was not standardized in the study and a prior encounter with a prey cannot be excluded, a limited probability of such incident and adequate, prey-specific reactions of randomly chosen spiders and prey suggest that in all likelihood the observed prey-catching behavior and prey recognition may be considered as pre-programmed.

The presence of prey specific modes of hunting manifested in four aspects of predatory technique: a) speed of approach, b) direction of approach, c) jumping distance, and d) other prey specific behaviors suggests that the alternative hunting tactics belong to a conditional strategy (Gross 1996; Gross & Repka 1998). Distinctive prey-specific capture behavior is often stressed to be typical for two groups of salticids (Li & Jackson 1996; Nelson et al. 2005): araneophagic species (e.g., Jackson 1992) and myrmecophagic species (e.g., Jackson & van Olphen 1992). In fact, all euryphagous jumping spiders tested with different prey types were found to possess prey-specific predatory tactics (Freed 1984; Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2007), which suggests that versatility may be a common feature among all Salticidae.

The young spiders discriminated between the prey with high and low ability to escape, and hunted them in a different way, which implies that the spiders possess not only complicated hunting behaviors that are dependent on prey type, but can also precisely recognize the prey. The modes of hunting caterpillars and leafhoppers correspond with the assumptions about how the prey that is able to effect escape or unable to do so should be pursued and captured (Bear & Hasson 1997). Thrips were, however, treated in an intermediate way. The spiders' movement pattern was simplified, without any behaviors reducing their visibility to the prey – typical for hunting caterpillars. Spiders approached generally without *stalk* or *movement masking* and with frequency of *frontal approach* between that of thrips and larvae. On the other hand they were not temporarily released after venom injection. The differences in the way thrips were preyed upon may suggest that the salticids can flexibly choose certain elements out of the available repertoire to maximize hunting success.

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Palpimanoid spiders from the Jurassic of China

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Abstract. Only two specimens of spiders have been described from Jurassic strata, so the recovery of some 400 new specimens from rocks of middle Jurassic age from China signals a dramatic increase in information on fossil spiders of this period. Here, new spiders belonging to the superfamily Palpimanoidea *sensu* Forster & Platnick 1984, from the locality of Daohugou, Inner Mongolia, are described. *Patarchaea muralis* n. gen., n. sp. is a true archaeid, represented by both an adult male and female. *Sinaranea metaxyostraca* n. gen., n. sp., represented by an adult male and juveniles, is a palpimanoid similar to Palpimanidae and Huttoniidae, but is not placed in a modern family.

Keywords: Archaeidae, Palpimanoidea, Middle Jurassic, Daohugou, China

Only two specimens of spiders have been described from rocks of Jurassic age (ca 145–200 mya): *Jurarchaea zherikhini* Eskov 1987 from Kazakhstan, which has been described as an archaeid, pararchaeid, or holarchaeid (Eskov 1987), and the araneoid *Juraraneus rasnitsyni* Eskov 1984 from Transbaikalia. A third, from the Jurassic of Grimmen, Germany, has been figured but not yet formally described (Ansorge 2003; preliminary investigation by the senior author suggests this may be a palpimanoid). Recently, more than 400 new specimens have become available for study from beds of Middle Jurassic age at Daohugou, Nincheng County, Inner Mongolia, China (Huang et al. 2006). Most belong to Uloboridae and will be the subject of another publication; the specimens described here belong in the superfamily Palpimanoidea *sensu* Forster & Platnick 1984, due to the presence of peg-teeth on the promargin of the chelicera.

The family Archaeidae Koch & Berendt 1854 is unique in that it was first described from fossils in Baltic amber (Koch & Berendt 1854), and some 25 years later living representatives were discovered in Madagascar (Pickard-Cambridge 1881). In the following century, living species have been described from other parts of Gondwana, and fossils described from strata of Mesozoic age: Cretaceous (Penney 2003) and Jurassic (Eskov 1987). The original family Archaeidae was divided into four families by Forster & Platnick (1984): Mecysmaucheniidae Simon 1895, Holarchaeidae Forster & Platnick 1984, and Pararchaeidae Forster & Platnick 1984, in addition to the type family. Archaeidae consists of small to medium-sized haplogyne ecribellate araneomorphs that are distinguished from other spiders by the character combination of peg-teeth on the promargin of the chelicera and an abdomen–petiole stridulatory system (Forster & Platnick 1984). Other features of the family, shared by some related families, are: stridulatory ridges on the lateral side of the chelicera, a raised cephalic region of the carapace, and chelicerae arising from a foramen in the clypeus, which is fully sclerotized ventrally in adults (Forster & Platnick 1984). These authors expanded the concept of the superfamily Palpimanoidea from its original size (formerly only Palpimanidae Thorell 1870, Stenochilidae Thorell 1873, and Huttoniidae Simon 1893) by the addition of three families, Mimetidae Simon 1881, Textricellidae Hickman 1945, and Micropholcommatidae Hickman 1944, previously placed in the Araneoidea Latreille 1806, as well as the four families in the original Archaeidae. Later, Platnick & Forster (1986) placed Textricellidae as junior synonym of Micropholcommatidae, and Platnick & Forster (1987) added Malkaridae Wunderlich 1986 to the Palpimanoidea. Two cheliceral characters were proposed as synapomorphies for the enlarged superfamily Palpimanoidea by Forster and Platnick (1984): the presence of peg teeth (modified setae) on the promargin of the cheliceral furrow, and the presence of an elevated cheliceral gland mound. The occurrence of peg teeth in other, unrelated, Araneomorphae were regarded as convergent features. In addition to these extant families, the fossil families Lagonomegopidae Eskov & Wunderlich 1995 and Spatiatoridae Petrunkevitch 1942 were included in Palpimanoidea by Eskov & Wunderlich (1995) and Wunderlich (1986), respectively.

Since the controversial expansion of the Palpimanoidea by Forster & Platnick (1984), several authors have studied the relationships of families within the superfamily. Schütt (2000, 2003) showed that the micropholcommatids and textricellids have spigots more similar to symphytognathids and that Mimetidae, Pararchaeidae, and Malkaridae should be removed from Palpimanoidea and placed in Araneoidea. The study of entelegyne spider phylogeny by Griswold et al. (2005) indicated that the extended Palpimanoidea was likely paraphyletic, with numerous families more probably belonging in Araneoidea. Most likely, the haplogyne palpimanoid families Archaeidae, Huttoniidae, Palpimanidae, and Stenochilidae really do belong in that superfamily, while the entelegyne palpimanoids, Holarchaeidae, Pararchaeidae, and Mimetidae are araneoids. Wunderlich (2004) recognized a number of palpimanoid families within his newly defined and expanded Eresoidea. The fossils described here do not provide evidence for any of these hypotheses, but they ean be accommodated

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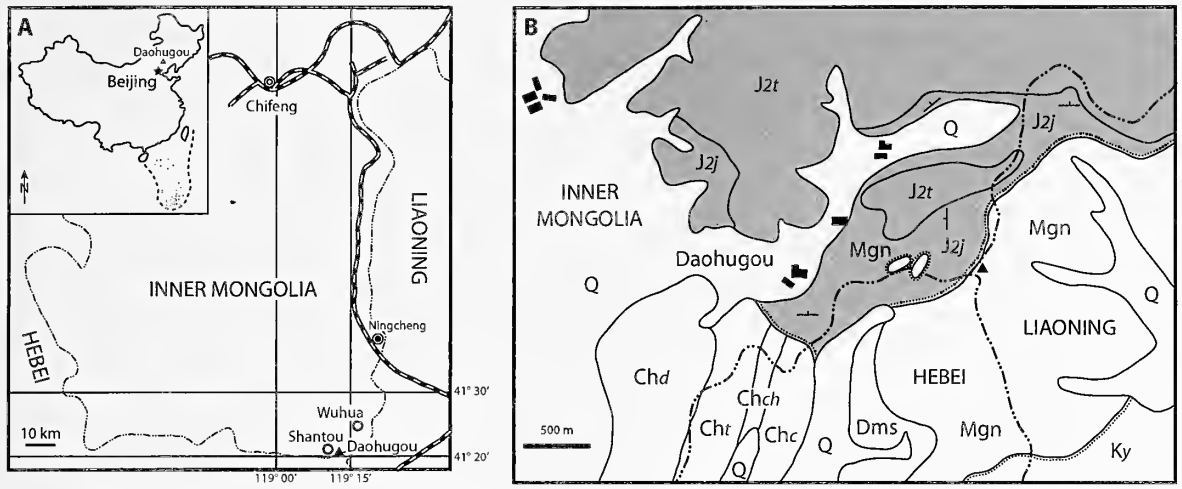


Figure 1.—Location and geological maps of the Daohugou locality. A. Location map of Daohugou village in Inner Mongolia and (inset) within China. B. Simplified geological map of the Daohugou area at the junction of three provinces. Dashed lines = province boundaries; solid lines = geological boundaries (solid + dotted line = unconformity between Precambrian and Mesozoic strata); shaded area = Jurassic (with strike/dip symbols). Precambrian formations: Mgn = Maanshan gneiss, Dms = Dalaiyingzi metamorphic series, Ch*c* = Changchougou Fm., Ch*ch* = Chuanlinggou Fm., Ch*d* = Dahongyu Fm., Ch*t* = Tuanshanzi Fm.; Mesozoic Formations: J2*j* = Jiulongshan Fm., J2*t* = Tiaojishan Fm., K*y* = Yixian Fm., Q = Quaternary. After Ren et al. (2002) and Gao & Ren (2006).

within the Palpimanoidea *sensu stricto*. *Patarchaea muralis* n. gen., n. sp., belongs in Archaeidae, and *Sinaranea metaxyostraca* is a palpimanoid with similarities to Palpimanidae and Huttonoiidae.

Among the palpimanoid families (s.l.), Malkaridae and Stenochilidae have no fossil record. *Jurarchaea*, from the Jurassic of Kazakhstan, has been described as a possible holarchaeid or pararchaeid (see Penney 2003); these families would otherwise have no fossil record. Mimetidae is known from Baltic and Ukraine amber (Wunderlich 2004), and the strictly fossil family Spatiatoridae occurs in Baltie amber (Petrunkevitch 1942; Wunderlich 2006). Another wholly fossil family, Lagonomegopidae, is known from Cretaceous ambers from Siberia (Eskov & Wunderlich 1995), Canada (Penney 2004), New Jersey (USA) and Myanmar (Penney 2005), and Spain (Penney 2006). A huttoniid has been described from Cretaceous Canadian amber (Penney & Selden 2006). Palpimanidae has been described from the Oligocene of Aix-en-Provence, France (Gourret 1888) and Miocene Dominican amber (Wunderlich 1988). Micropholcommatidae has recently been described from Eocene amber of France (Penney et al. 2007), and the first fossil mecysmaucheniid has been described from Cretaceous amber of France (Saupe & Selden in press). Penney (2003) listed *Baltarchaea conica* (Koch & Berendt 1854), from Eocene Baltic amber, as a mecysmaucheniid following a suggestion by Eskov (1987); however, the specimen has been lost, so its identity cannot be checked. First described from Eocene Baltic amber (Koch & Berendt 1854), archaeids have a fossil record that extends from the Recent back to the Jurassic (Eskov 1987; this paper). Within this range, archaeids are known from sub-Recent Madagasean copal (Lourenço 2000), many in Cenozoic Baltic amber (Wunderlich 2004) and Cretaceous Burmese amber (Penney 2003), but not Dominican amber – the specimen reported as Archaeidae by Wunderlich (1999), supposedly a fossil in Dominican amber, is actually a subfossil preserved in Madagascan copal (Wunderlich 2004; Penney & Langan 2006)

METHODS

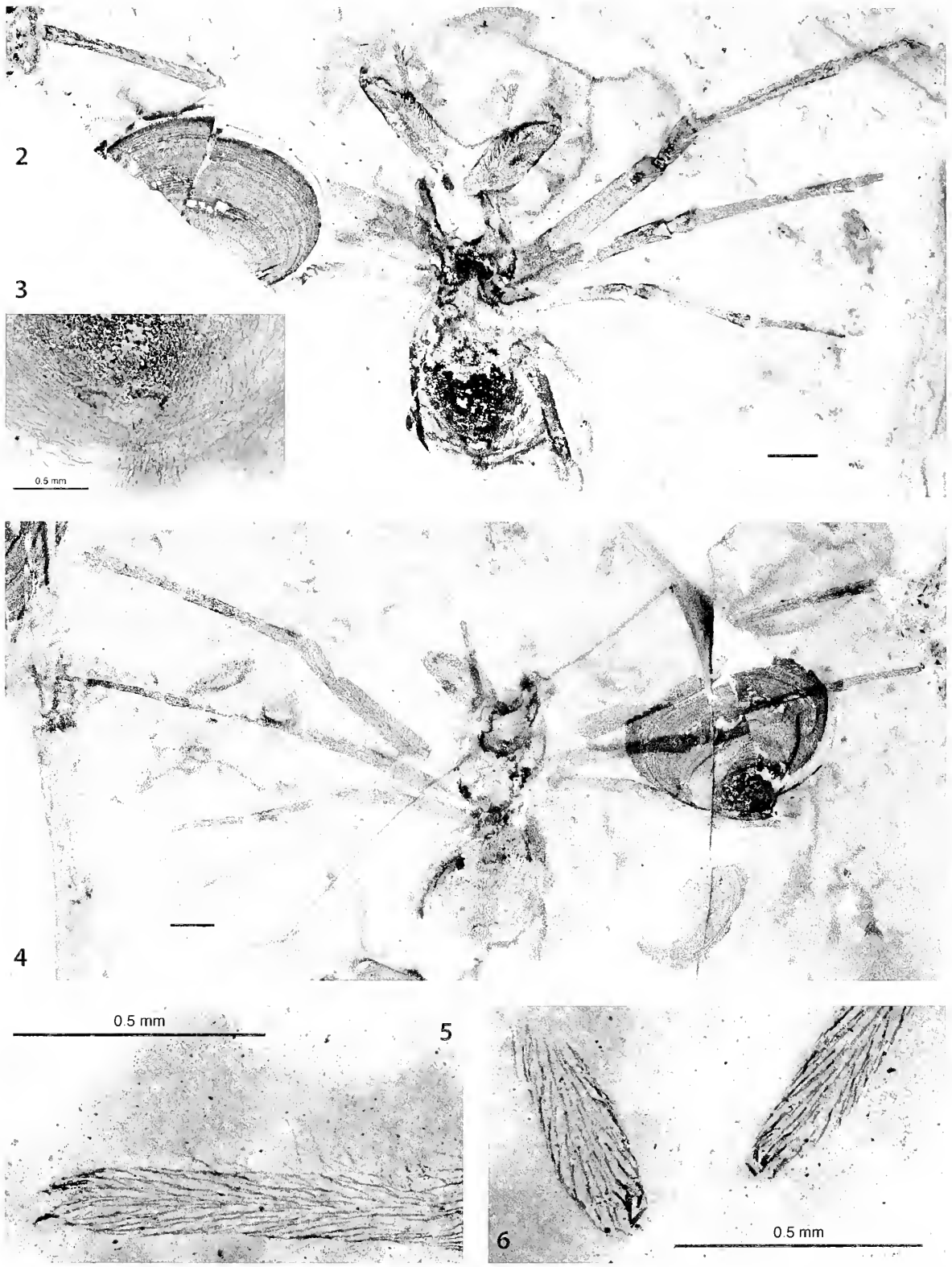
Material.—The spiders are preserved in a finely laminated, pale gray siltstone which represents a lacustrine deposit. On many bedding planes, the matrix is characteristically crammed with conchostracans and insects. The spiders are preserved as brown material compressed within the siltstone. Locality details are shown in Figure 1, and can be found in Ren et al. (2002). Recent evidence, which places the strata in the Jiulongshan Formation, and discussion of its age, is given in Chen et al. (2004) and Gao & Ren (2006). Eight specimens are described here, seven of which (prefixed NIGP) are held in the collections of the Nanjing Institute of Geology and Palaeontology, the other (prefixed SIM) is in the collections of the College of Life Science, Capital Normal University, Beijing. PAS is responsible for the arachnological studies; the other authors discovered the specimens and provided study facilities for PAS in China.

Methods.—The preparation of most of the spiders (NIGP specimens) was carried out by Huang Diying using a small chisel and a sharp knife. An aeroneedle (Selden 2003) was used to prepare specimen SIM2005003. Photomicrographs were made using a Nikon D1X digital camera on Leica MZ microscopes and manipulated in Adobe Photoshop. Drawings were prepared using a drawing tube on the microscope and also by tracing from photographs with Adobe Illustrator. All measurements are in mm, and were made using Carnoy 2.1 (Schols et al. 2002) for *Patarchaea*, and measuring tools in Photoshop CS3 Extended for *Sinaranea*.

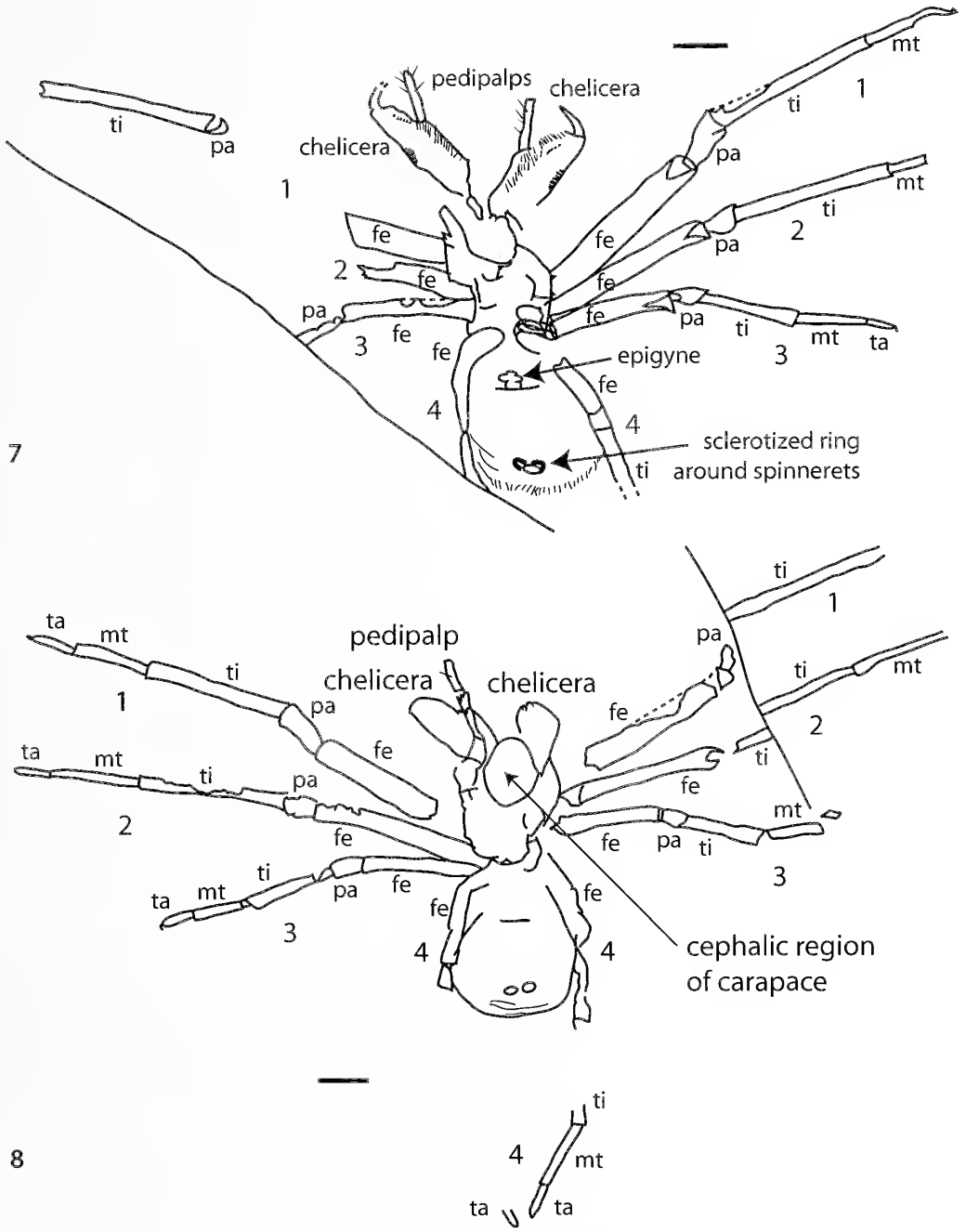
Abbreviations used in the Figures.—1, 2, 3, 4 = leg numbers, conch = conchostracan, cx = coxa, e & c = embolus and conductor, fe = femur, mt = metatarsus, pa = patella, st = sternum, strid. file = stridulatory file, ta = tarsus, te = tegulum, ti = tibia.

INTERPRETATION OF THE FOSSILS

The cephalic region of the carapace of the holotype of *Patarchaea* was presumed to have been raised in life because the fossils show a ring of cuticle infilled with a white mineral; thus the head region is preserved inside the rock matrix. The



Figures 2–6.—*Patarchaea muralis* new genus and species. Holotype adult female. NIGP148828a (part) and NIGP148828b (counterpart), Jurassic of China. 2. Part, whole; 3. Spinnerets of part; 4. Counterpart whole (except leg 4 tarsi); 5. Counterpart left tarsus 1; 6. Counterpart left and right tarsi 4. Scale = 1.0 mm unless stated otherwise.



Figures 7, 8.—*Patarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part) and NIGP148828b (counterpart), Jurassic of China. 7. Camera lucida drawing of part, explanatory drawing for Figure 2; 8. Camera lucida drawing of counterpart, explanatory drawing for Figure 4. Scale = 1.0 mm.

fossil has suffered some compression so that the chelicerae are divergent on the bedding plane. In all of the fossils, there is evidence, in the form of crumpling and skewing, that the head region was raised, but without an elongated neck.

An interesting feature in NIGP148238 is the presence of two patches of small, circular objects which have been identified here as conchostracan ova (Shen & Huang 2008).

TAXONOMY

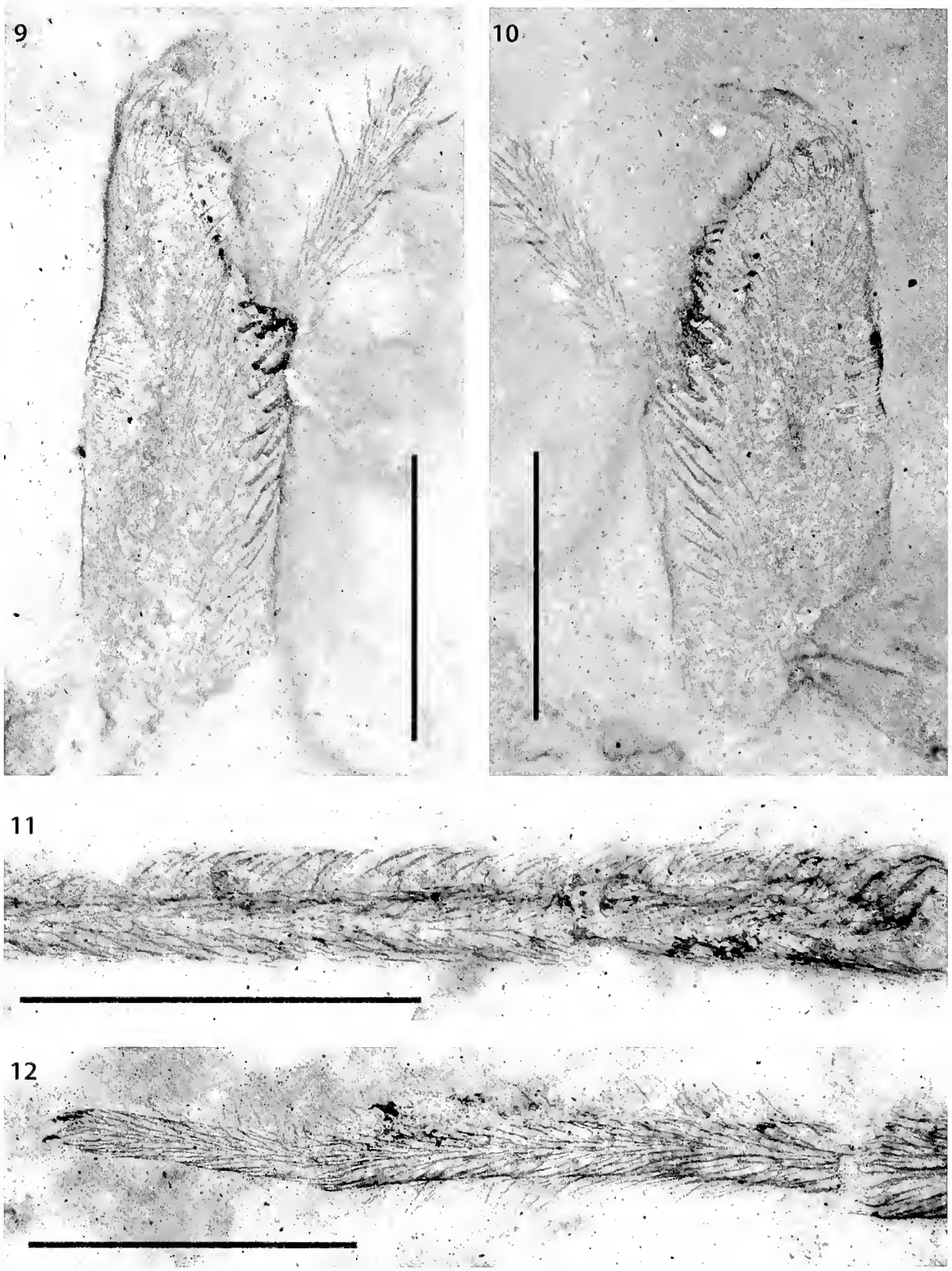
Superfamily Palpimanoidea *sensu* Forster & Platnick 1984
Family Archaeidae Koch & Berendt 1854
Patarchaea new genus

Type species.—*Patarchaea muralis* new species

Diagnosis.—Archaeid with pair of sclerotized lunules round anterior side of spinnerets, rather than completely encircling spinnerets; male pedipalp with large, thick spine arising from cymbium.

Etymology.—Greek *patos*, a beaten path, and *Archaea*, the type genus of Archaeidae.

Remarks.—*Patarchaea* can be referred to the family Archaeidae on account of the long, slender legs lacking macrosetae; leg 1 being especially longer and stouter than the others, with a conspicuously long patella and spatulate setae on the tibia and metatarsus; three tarsal claws; long, slender



Figures 9–12.—*Patarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part) and NIGP148828b (counterpart), Jurassic of China. 9. Left chelicera of part; 10. Right chelicera of part; 11. Right tibia 1 of part, showing curved, spatulate setae; 12. Left metatarsus and tarsus 1 of counterpart (i.e., same leg as in Figure 11). Scale = 1.0 mm.

chelicerae with peg-teeth on the promargin extending back down much of the length of the paturon, true teeth on the retromargin, short, curved fang, cheliceral gland mound near the fang tip, stridulatory ridges; and sclerotized semicircles in front of the spinnerets. Closely related families differ in the following ways. In Pararchaeidae leg 1 is not markedly slender and lacks scopulae, the first leg patella is not conspicuously long; the chelicerae have peg-teeth on the promargin but the

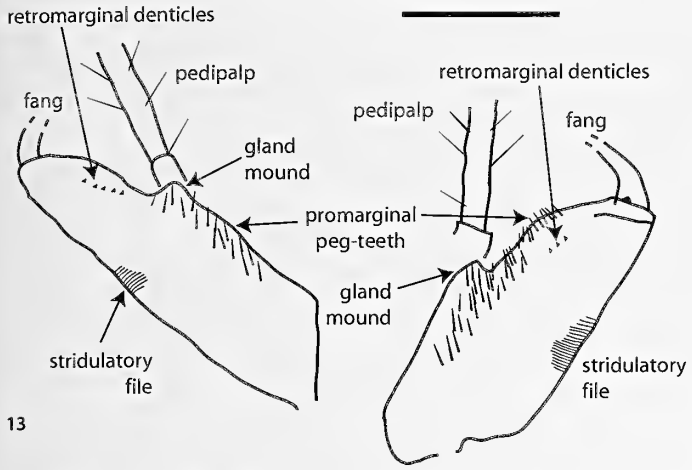


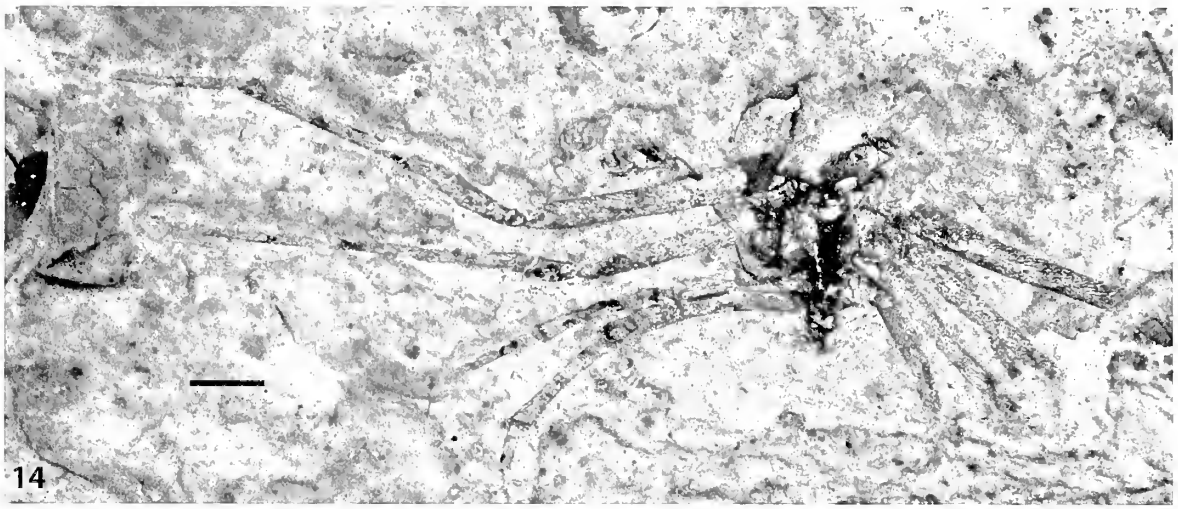
Figure 13.—*Patarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part), Jurassic of China, camera lucida drawing of chelicerae, explanatory drawing for Figures 9–10.

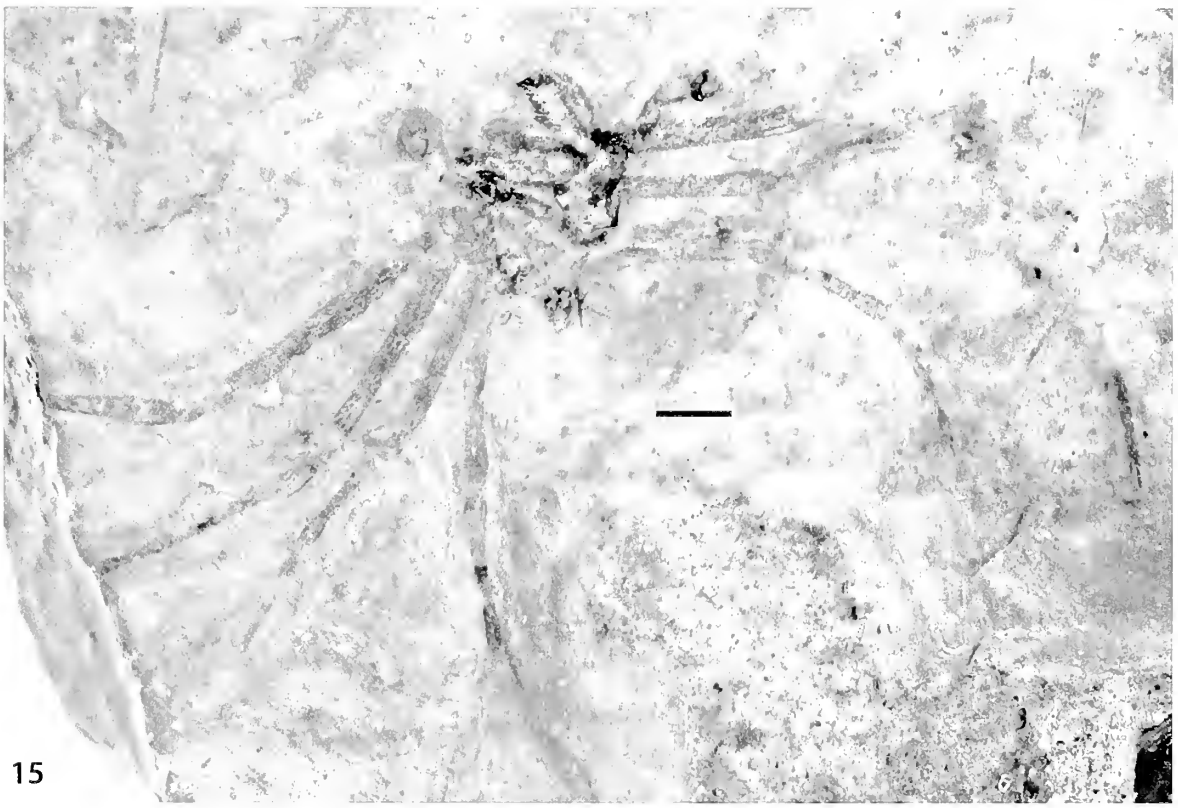
retromargin lacks teeth or denticles; there is a pronounced keel down the ventral side of the paturon beyond the fang tip; and there is no sclerotized ring around the spinnerets. Holarchaeids are minute; leg 1 lacks scopulae and the tarsi of legs 1 and 2 are swollen and have a patch of modified setae; patella 1 is not conspicuously long; the chelicerae lack peg-teeth though there are a few slender teeth on the promargin; there are no stridulatory ridges on the chelicerae nor a sclerotized ring around the spinnerets. The first legs in Mecysmaucheniidae lack scopulae and the patella is not especially elongate; the peg-teeth on the cheliceral promargin do not extend down the paturon and there are no teeth on the retromargin; there is no sclerotized ring around the spinnerets in modern forms.

There are three deseribed extant genera of Archaeidae: *Afrarchaea* Forster & Platnick 1984, *Austrarchaea* Forster & Platnick 1984, and *Eriauchenius* O. Pickard-Cambridge 1881 (Lotz 2006). Wunderlich (2004) listed six fossil genera, all from Baltic amber. The Jurassic *Jurarchaea* Eskov 1987, from the Jurassic of Kazakhstan, which Wunderlich (2004) eonsidered to be too poorly preserved to be identified as an archaeid, most likely belongs close to Pararchaeidae and Holarchaeidae, where it was placed by Eskov (1987) (Penney 2003). Eskov (1992) described *Mimetarchaea gintaras* from Baltic amber from a specimen that supposedly possesses key apomorphies of the families Archaeidae *seusu lato* (modified chelicerae and carapace) and Mimetidae (metatarsal macrosetal brush), and he placed *Mimetarchaea* close to Pararchaeidae or Holarchaeidae. Eskov (1990) had suggested that Mimetidae and Archaeidae form a sister pair within the Palpimanoidea, and thus more closely related than was suggested by Forster & Platnick (1984). However, Wunderlich (2004) concluded that the holotype of *Mimetarchaea gintaras* was a subadult male, not an adult, and that the embolus described by Eskov (1992) was the margin of the palpal tarsus. Wunderlich placed the specimen in Mimetidae, even considering it to belong to the extant genus *Mimetus* and stated that Eskov's speculations regarding the relationships between Archaeidae and Mimetidae were invalid. In any case, *Patarchaea* does not possess the characteristic mimetid-like spines on the metatarsi of legs 1 and 2. Eskov (1992) erected the genus *Baltarchaea* Eskov 1992 for the Baltic amber *Archaea conica* Koch & Berendt 1854; the type specimen of which is lost, but Wunderlich (2004, photos 66, 67) figured specimens which he considered belong in this genus. *Baltarchaea* is characterized by a squat carapace with a pair of posterior cephalic projections and short legs and chelicerae, and was placed in Mecysmaucheniidae by Eskov (1992). *Archaea* differs from *Patarchaea* by its stridulating file being in the proximal half of the chelicera (Wunderlich 2004) and the more elongated head region. The genus *Eoarchaea* Forster & Platnick 1984 was erected for the very small species *Archaea hyperoptica* Menge, in Koch and Berendt 1854 from Baltic amber which lacks the elongated head region of other archaeids. Forster & Platnick (1984) suggested that the genus was known only from juveniles, and Eskov (1992) synonymized *Eoarchaea* with *Archaea* on this basis. However, Wunderlich (2004) considered the genus to be valid and the specimens (more of which are now available in both Baltic and Bitterfeld amber) to be small females due to their general proportions and the fact that many specimens of the same size have been found; no genital organs, nor males, have been found. Regardless of whether the genus is a valid one, it differs from *Patarchaea* by the very short carapace; in *Patarchaea*, while the head region is unlikely to be strongly elongated, the total carapace length is about twice that of the head region. *Myrmecarchaea* Wunderlich 2004 was erected for a group of archaeids with an extremely elongated petiolus and, thus, a general resemblance to ants. *Saxonarchaea* Wunderlich 2004 differs from *Patarchaea* by its more greatly elongated anterior legs and chelicerae and small cymbium in the male.

Eriauchenius was the first living archaeid to be described (Pickard-Cambridge 1881), albeit as a theridiid. The genus was placed in synonymy with *Archaea* Koch & Berendt 1854 by Forster & Platnick (1984), but removed from this synonymy by Wunderlich (2004) on the basis of the position of the stridulating file on the chelicera: it is in the distal half in *Eriauchenius* (and *Austrarchaea*), the proximal half in *Archaea*. Eskov (1992) synonymized *Archaea* and *Afrarchaea* but this synonymy was not accepted by later workers (Penney 2003; Lotz 2006). Wunderlich synonymized *Afrarchaea* and *Eriauchenius*, on the basis of similarity in the male palps, a decision not followed by Lotz (2006). *Afrarchaea* has a much lower head region without a constricted neck, in comparison with *Archaea* and *Eriachenius* (Lotz 2006).

Of all archaeid genera, *Patarchaea* most resembles *Afrarchaea* on the following characters. The head region is not greatly elongated, the position of the stridulating file is in the distal half of the chelicera, the presumed large cheliceral gland mound resembles the triangular process on the male chelicera of the type species *Afrarchaea godfreyi* (Hewitt 1919) (Lotz 1996, fig. 6). *Patarchaea* differs from *Afrarchaea* in its longer carapace, as well as in the diagnostic features listed above. Although not mentioned by the authors in the text, a distinct bend in the fourth femur can also be seen in *Afrarchaea* and *Eriauchenius*: *Afrarchaea royalensis* Lotz 2006 (Lotz 2006, fig. 8), *A. woodae* Lotz 2006 (Lotz 2006, fig. 11), *A. grimaldii* Penney 2003 (Penney 2003, fig. 1), *Eriauchenius cornutus* (Lotz 2003) (Lotz 2006, fig. 1), *E. gracilicollis* Millot 1948 (Wunderlich 2004, fig. 44; pls. 81, 82). In a recent paper on the *Eriauchenius gracilicollis* group from Madagascar the distinctly curved fourth femur is listed in the genus description and





Figures 14, 15.—*Patarchaea muralis* new genus and species. Allotype adult male, SIM2005003-1 (part) and SIM2005003-2 (counterpart), Jurassic of China. 14. Counterpart, whole; 15. Part, whole. Scale = 1.0 mm.

illustrated (Wood 2008: fig. 7D). In correspondence, Wood (February 2008) provided the information that the curved fourth femur is pronounced in archaeids and also occurs, to a lesser extent, in mecysmaucheniids. Its function may be to aid in closely adpressing the leg against the rotund abdomen when at rest.

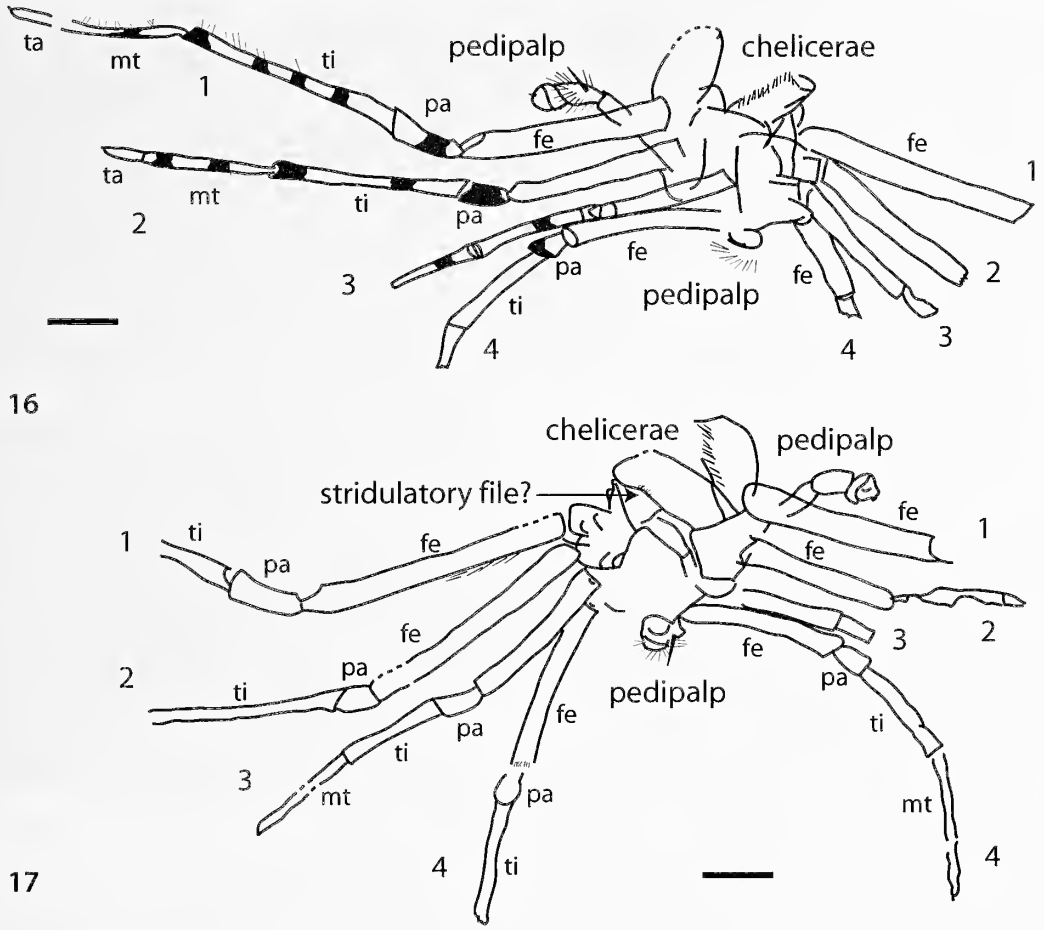
Patarchaea muralis new species
Figs. 2–24

Material examined.—Holotype: NIGP148828a, b (part and counterpart), adult female, from laminated siltstones of the Middle Jurassic Jiulongshan Formation, Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China (41°19.532′N, 119°14.589′E). Allotype: SIM2005003-1 and SIM2005003-2 (part and counterpart), adult male, from the same locality. Additional specimen NIGP148829, adult female, from the same locality.

Diagnosis.—As for the genus.

Etymology.—Latin *murus*, a wall; in combination with the prefix to the genus name, in memory of a wonderful day in great company walking along the Great Wall of China.

Description of holotype, NIGP148828a,b (Figs. 2–13).—Adult female. Carapace with raised cephalic area; eyes not seen. Carapace length 2.51, width 1.98; head region length 1.37, width 1.07. At least two thorns on carapace lateral margin. Chelicera long (paturon length 2.33) with prominent

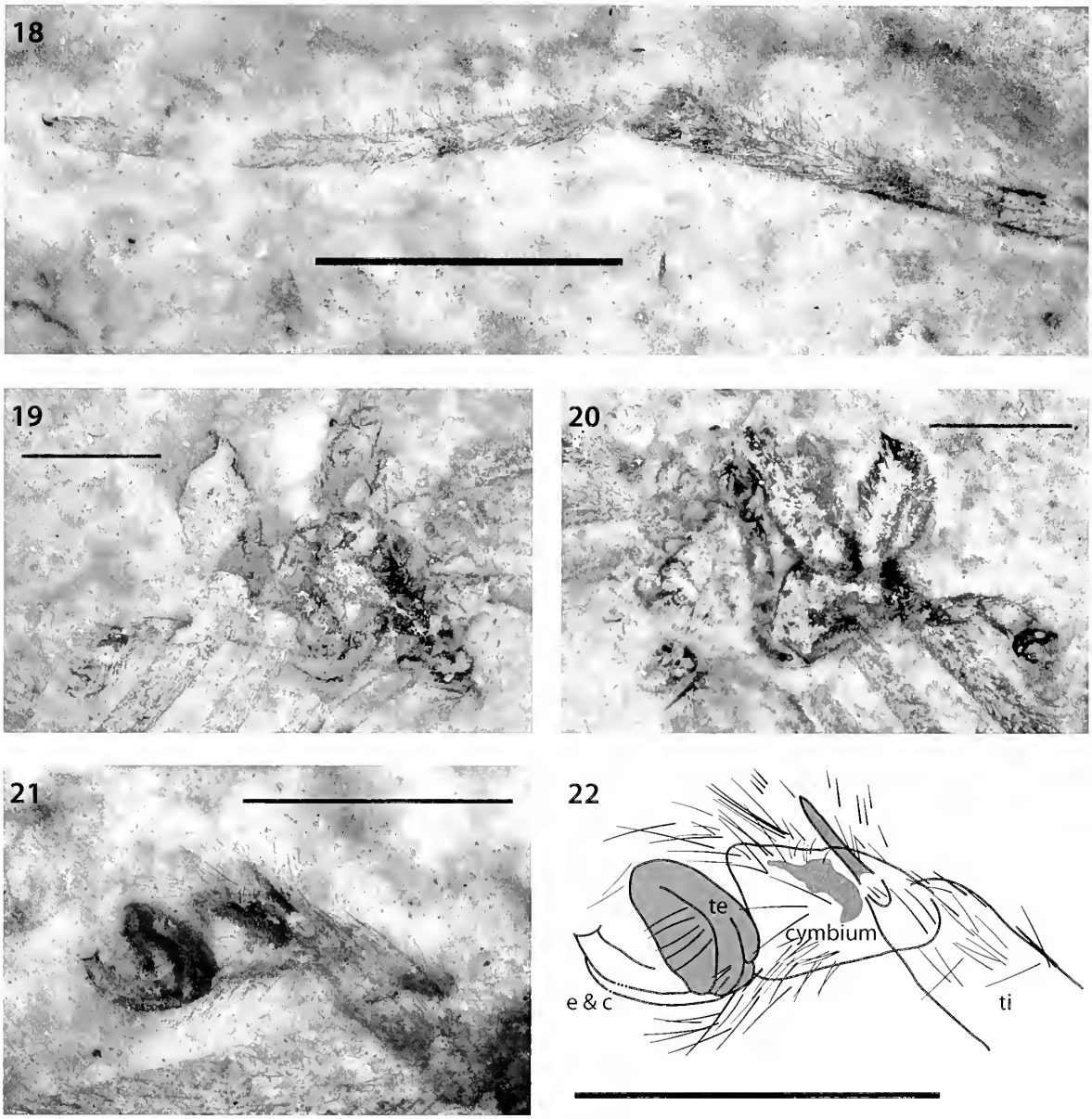


Figures 16, 17.—*Patarchaea muralis* new genus and species. Allotype adult male, SIM2005003-1 (part) and SIM2005003-2 (counterpart), Jurassic of China. 16. Camera lucida drawing of counterpart, explanatory drawing for Figures 14 and 19; 17. Camera lucida drawing of part, explanatory drawing for Figures 15 and 20. Scale = 1.0 mm.

cheliceral gland mound just less than half cheliceral length from base of fang. Cheliceral groove with at least five retromarginal denticles and many promarginal peg-teeth extending from near base of fang to near base of paturon (c. ¾ length of paturon). Normal setae also present. Stridulatory file situated mid-way between base of fang and base of chelicera, on ectal margin (approximately on opposite side of paturon from cheliceral gland mound). Fang thickened at base. Pedipalp at least as long as chelicera, with at least six macrosetae on tarsus. Leg formula 1243. Podomere lengths: leg 1 femur 3.44, patella 1.07, tibia 3.12, metatarsus 1.46, tarsus 0.99; leg 2 femur 3.21, patella 0.67, tibia 2.97, metatarsus 1.76, tarsus 0.72; leg 3 femur 2.27, patella 0.60, tibia 1.72, metatarsus 1.30, tarsus 0.68; leg 4 femur 3.09, patella 0.43, tibia 2.07, metatarsus 1.35, tarsus 0.74. Leg 1 noticeably longer and more robust than other legs: femur thicker, patella longer and more robust, and tibia longer. Leg 4 femur distinctly bent. All leg podomeres lack macrosetae; leg 1 with scopula of curved, spatulate setae on tibia, continues with fine, erect setae on metatarsus and tarsus. Three tarsal claws. Opisthosoma pyriform in dorsal aspect, with blunt posterior margin; length 3.54, width 2.39 at widest point close to posterior margin. Epigynum subtriangular, apex pointing anterior, posterior corners each with a distinct c-shaped ?receptaculum. Ventral cuticle between epigynum and spinnerets rugose. Pair of curved, sclerotized ridges in anterolateral part of spinneret region.

Description of allotype, SIM2005003-1/2 (Figs. 14–22).—Adult male. Carapace not preserved. Chelicera 1.47 long; many promarginal peg-teeth extending from near base of fang to near base of paturon. Pedipalp tibia elongate; cymbium with massive, straight macroseta arising from base; large bulb (tegulum) with distal embolus and conductor. Leg formula 1243. Podomere lengths: leg 1 femur 3.44, patella 1.13, tibia 3.26, metatarsus 1.84, tarsus 0.78; leg 2 femur 2.93, patella 0.64, tibia 2.82, metatarsus 1.92, tarsus 0.58; leg 3 femur 2.00, patella 0.49, tibia 1.61, metatarsus 1.47; leg 4 femur 2.37, patella 0.49, tibia 1.65, metatarsus 1.33, tarsus 0.80. Leg 1 noticeably longer and more robust than other legs; patella longer and stouter, metatarsus slightly curved. Leg 4 femur distinctly curved. Legs annulated: at least patella, tibia, and metatarsus with up to three dark annulae. All leg podomeres lack macrosetae; leg 1 with sparse scopula of fine, erect setae on tibia, metatarsus, and tarsus. Opisthosoma not preserved.

Description of additional specimen, NIGP148829 (Figs. 23, 24).—Adult female. Carapace very poorly preserved; outline of raised head region with subcircular cross-section, ≤ 1.58 long; outline of carapace subparallel-sided, 3.62 long, 2.26 wide. Chelicera ≥ 2.41 long; left chelicera shows few promarginal peg-teeth distally, stridulating file. Pedipalp



Figures 18–22.—*Patarchaea muralis* new genus and species. Allotype adult male, SIM2005003-1 (part) and SIM2005003-2 (counterpart), Jurassic of China. 18. Left distal tibia, metatarsus and tarsus of leg 1 of counterpart; 19. Detail of body showing chelicerae and pedipalps of counterpart, see Figure 16; 20. Detail of body showing chelicerae and pedipalps of part, see Figure 17; 21. Photograph combining left palp of counterpart superimposed on right palp of part; note massive, straight macroseta on tibia; 22. Explanatory drawing for Figure 21. Scale = 1.0 mm.

slender, left pedipalp tarsus with claw. Only proximal leg segments preserved. Podomere lengths: leg 1 femur 4.43, patella 1.28; leg 2 femur 3.77, patella 1.01; leg 3 femur 2.72, patella ≥ 0.80; leg 4 poorly preserved but femoral curve visible. Leg 1 noticeably longer and more robust than other legs. All visible podomeres lack macrosetae. Opisthosoma not preserved.

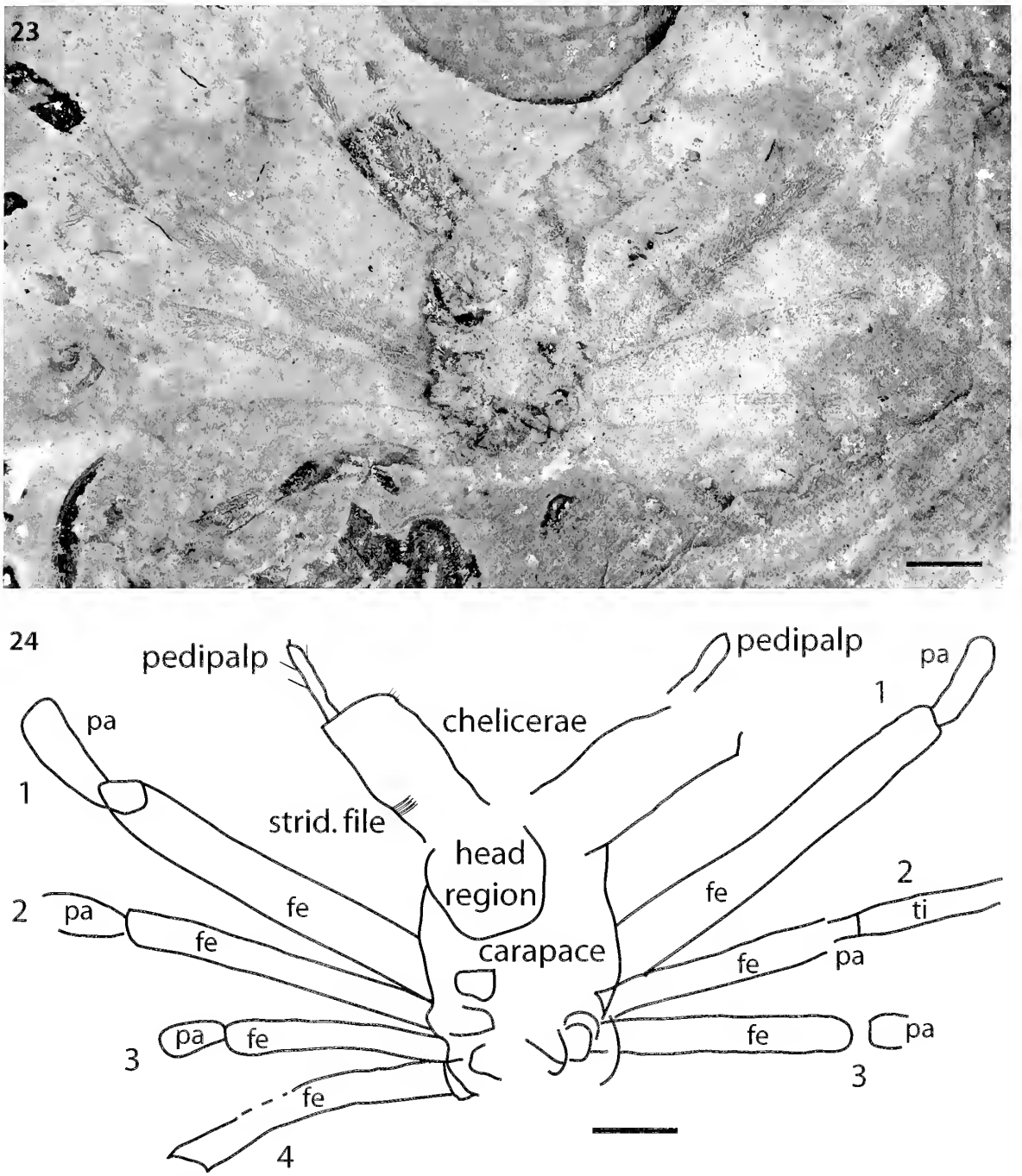
Family unknown
Sinaranea new genus

Type species.—*Sinaranea metaxyostraca* new species

Diagnosis.—Palpimanoid with a combination of elongate leg 1 patella and short leg 2 patella; carapace with raised cephalic area (cf. Huttoniidae) but apparently lacking rugose or tuberculate ornament (cf. Palpimanidae); scutum on dorsal opisthosoma.

Etymology.—Latin *Sinae* (after ancient Arabic *Sin*), China, and *aranea*, a spider.

Remarks.—*Sinaranea* can be referred to the Palpimanoidea on the basis of the cheliceral peg-teeth. The carapace is not diamond-shaped like in Stenochilidae, and has no greatly elongated neck as in Archaeidae, but it has a raised cephalic region, unlike the Huttoniidae; it seems to lack the strong sclerotization of Palpimanidae. The chelicerae are large, but not elongated, and the fang is short and transverse to the long axis of the cheliceral paturon, as in Palpimanidae and Huttoniidae. No stridulating ridges can be seen on the chelicerae in the fossils. The holotype is missing the distal podomeres of leg 1, so it is impossible to tell whether spatulate setae are present, but they seem to occur in NIGP148237, a probable juvenile. Overall, the genus resembles Palpimanidae



Figures 23, 24.—*Patarchaea muralis* new genus and species. Adult female, NIGP148829, Jurassic of China. 23. Photograph; 24. Camera lucida drawing, explanatory drawing for Figure 23. Scale = 1.0 mm.

and Huttoniidae more than other Palpimanoidea, but is not sufficiently well defined to be placed with certainty in either of these modern families. Indeed, it is possible that it could be ancestral, so no familial placement is proposed.

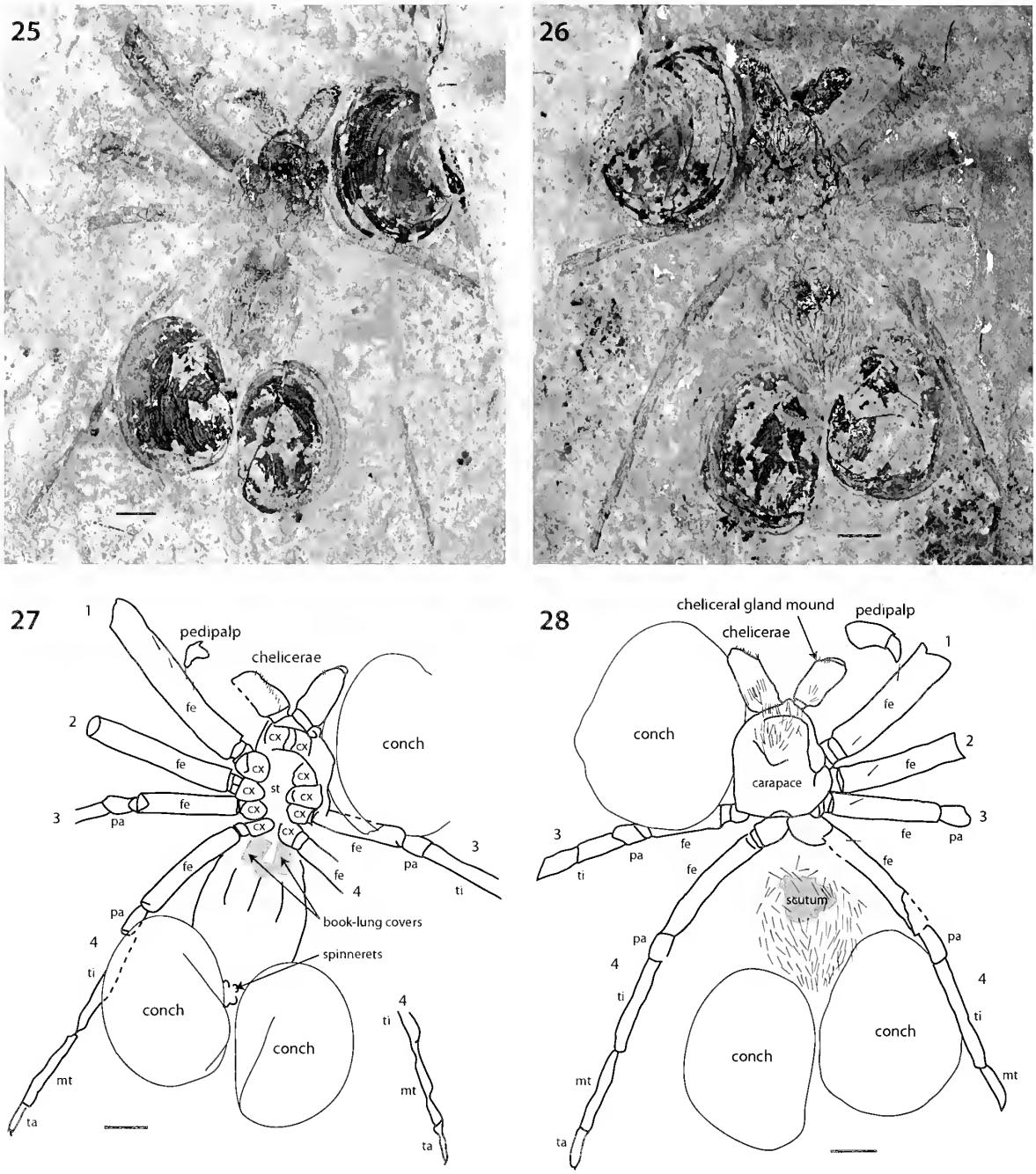
Sinaranea metaxyostraca new species
Figs. 25–40

Material examined.—Holotype: NIGP148830a,b (part and counterpart), adult male, from laminated siltstones of Middle Jurassic Jiulongshan Formation, Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China (41°19.532′N, 119°14.589′E).

Diagnosis.—As for the genus.

Etymology.—Greek *metaxy*, between, and *ostraca*, shells, in reference to the occurrence of the holotype between a number of conchostracan shells.

Remarks.—These five specimens are placed together in *Sinaranea metaxyostraca* on account of their similar habitus. The cephalic area of the carapace is noticeably raised, but not elongated or with a neck; the opisthosoma bears a small, subcircular dorsal scutum; the legs are short, with the formula 1243, and the patella of leg 1 is noticeably long, while that of leg 2 is distinctly short; the femur of leg 4 is not curved. Apart from the holotype, the specimens are preserved on the bedding

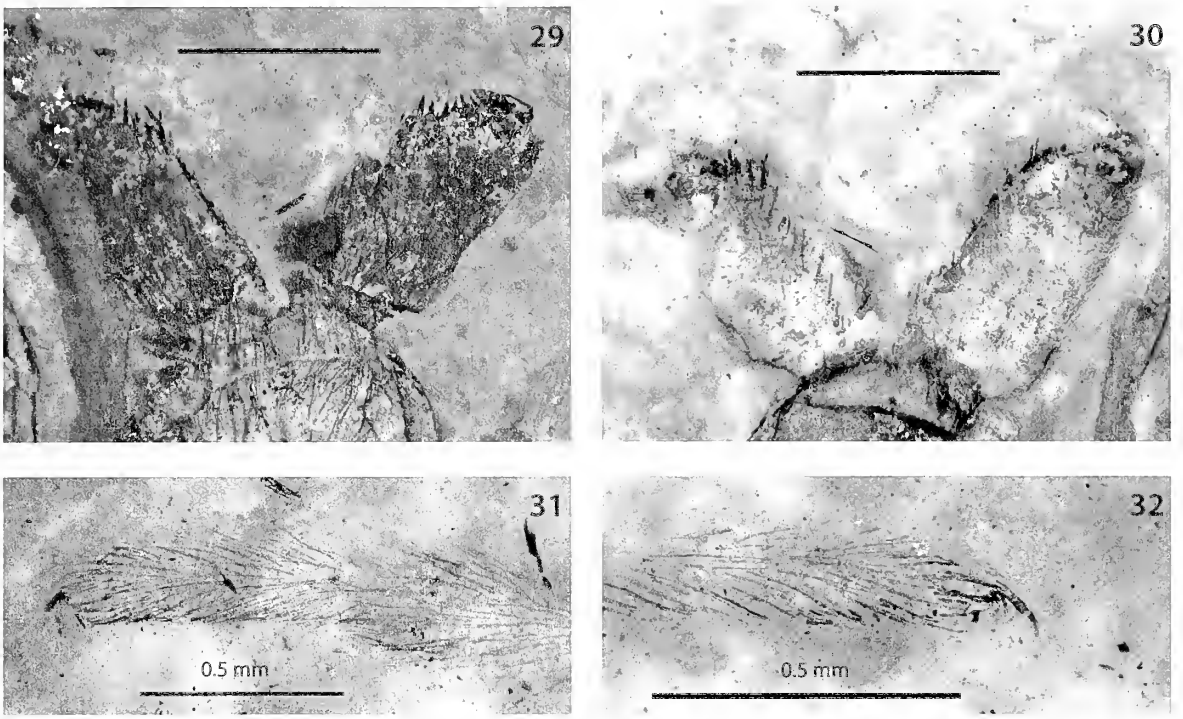


Figures 25–28.—*Sinaranea metaxyostraca* new genus and species. Holotype adult male, NIGP148830a (part) and NIGP148830b (counterpart), Jurassic of China. 25. Part, whole; 26. Counterpart, whole; 27. Camera lucida drawing of part, explanatory drawing for Figure 25; 28. Camera lucida drawing of counterpart, explanatory drawing for Figure 26. Scale = 1.0 mm.

planes of whitish-gray tuff at Xiayingzi in Daohugou Village. This fossil bed is easily recognized because it lacks the familiar conchostracans present on bedding planes with *Patarchaea*, but has anostracans and ova. The paleoecological significance of this not clear, but the two new genera reported here may not have lived in the same habitat.

The holotype is somewhat larger than the rest, and is probably an adult male because of the fragment of pedipalp, its larger size (hence likely mature), longer legs, and lack of an epigynum. The other specimens are most likely juveniles because adult female spiders are normally larger than adult males, and they show no sign of the development of modified palps, nor epigyna.

Description of holotype, NIGP148830a,b (Figs. 25–32).—Adult male. Carapace length 2.48, width 2.17, subrectangular, broadly recurved posterior margin, subparallel-sided, procurved anterior margin; distinctly demarcated anterior cephalic area, length 1.07, presumably raised in life. Chelicera subrectangular, somewhat elongated and robust, distal margin at right angle to ectal edge for first half of width, then turns c. 30° angle to meet mesal edge; fang extends across distal edge and along mesal angle; many peg-teeth extend from distal edge



Figures 29–32.—*Sinaranea metaxyostraca* new genus and species. Holotype adult male, NIGP148830a (part) and NIGP148830b (counterpart), Jurassic of China. 29. Counterpart, chelicerae; 30. Part, chelicerae; 31. Counterpart tarsus of left leg 4; 32. Part tarsus of right leg 4 (i.e., same tarsus as is Figure 31). Scale = 1.0 mm.

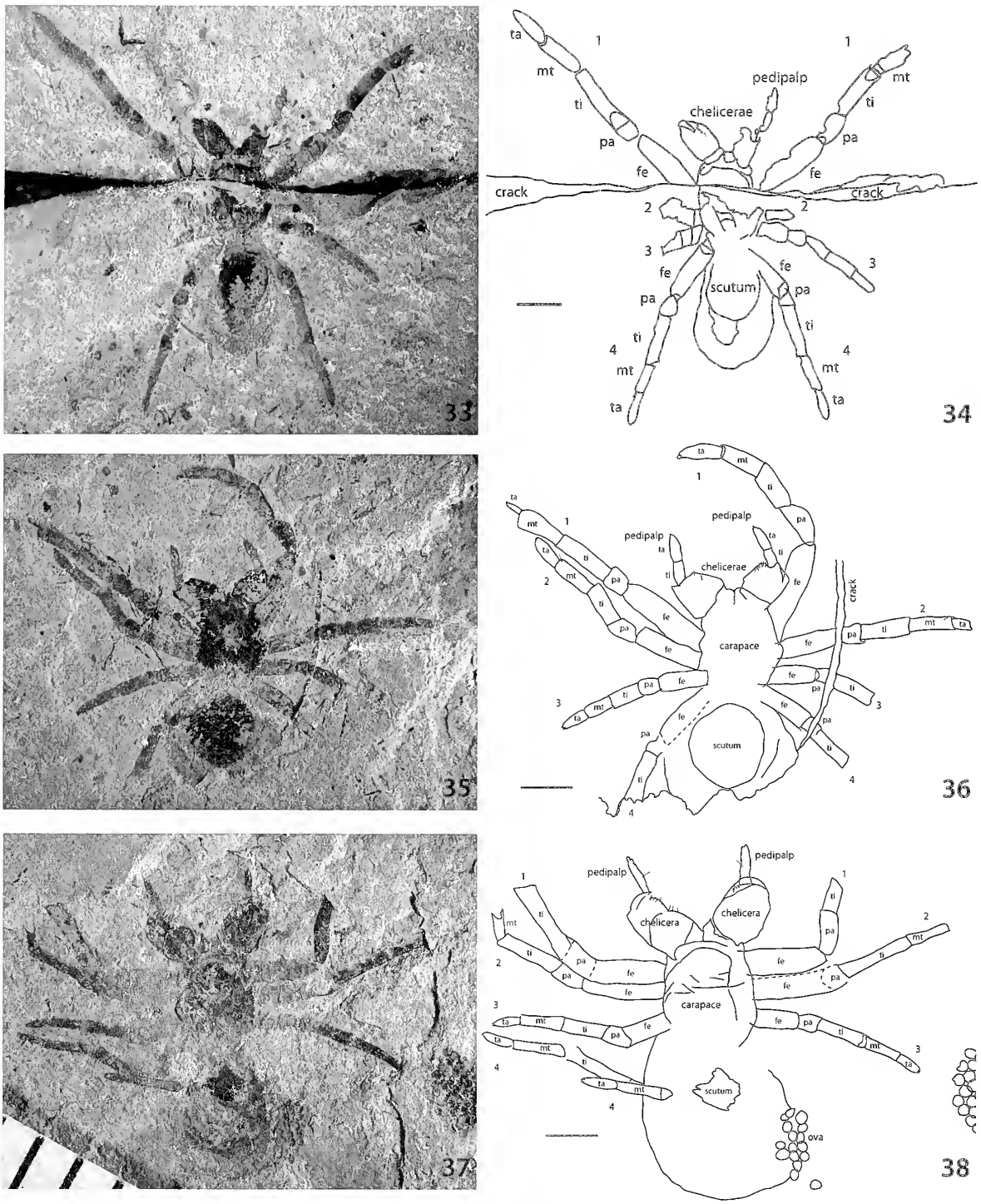
down full length of mesal edge; stridulatory organ (if present) not visible. Pedipalp poorly preserved but some sclerotization preserved at distal tip of right pedipalp suggests a modified male organ. Leg formula (based on femora) 1243. Podomere lengths: leg 1 femur 4.54; leg 2 femur 3.56; leg 3 femur 2.29, patella 0.70, tibia 1.69; leg 4 femur 2.85, patella 0.72, tibia 2.62, metatarsus 1.99, tarsus 0.90. Leg 4 femur curved but without distinct bend-point. Tarsus 4 with distinctly elongate paired claws, pectinate with at least 3 teeth basally; hook-like third claw. Opisthosoma suboval, length 3.68, width 2.50; dorsal scutum (NB: dark area between rear of book-lung covers on NIGP148830a (ventral), which superficially resembles an epigynum, is most likely the anterior part of the dorsal scutum cuticle superimposed on the ventral counterpart, as are patches of cuticle posterior to it). Spinnerets subterminal.

Description of additional specimen, NIGP148236 (Figs. 33, 34).—Juvenile? Carapace length 1.95, width 1.26, subrectangular to broadly suboval, raised head region clearly demarcated, 1.09 long. Chelicerae large, robust, with row of many peg-teeth extending from distal edge down length of mesal edge; length 1.18; curved fang visible on left side. Pedipalp poorly preserved on right side, clearly not bulbous. Legs short; leg formula 1243. Podomere lengths: leg 1 femur 1.81, patella 0.78, tibia 1.41, metatarsus 1.03, tarsus 0.98. Leg 2 poorly preserved. Leg 3 femur ≥ 0.69, patella 0.42, tibia 0.64, metatarsus 0.73, tarsus 0.60 (incl. claws). Leg 4 femur 1.33, patella 0.48, tibia 1.18, metatarsus 0.78, tarsus 0.78 (incl. claws). Opisthosoma length 2.85, width 1.80; scutum covers most of dorsal surface, remainder of cuticle setose. Spinnerets not preserved.

Description of additional specimen NIGP148237 (Figs. 35, 36).—Juvenile? Carapace length 1.75, width 1.60. Chelicerae large, robust, with peg-teeth extending from distal edge down length of mesal edge; length 0.96. Pedipalps on both sides not bulbous, tarsus with claw; tarsal length 0.55 (incl. claw). Legs short; leg formula 1243. Leg 1 right preserved in lateral aspect, palpimanid-like, apparently with scopulae on tibia–tarsus. Podomere lengths: leg 1 femur 1.73, patella 0.85, tibia 1.00, metatarsus 0.87, tarsus 0.87 (incl. claws). Leg 2 femur 1.40, patella 0.50, tibia 0.90, metatarsus 0.84, tarsus ≥ 0.64. Leg 3 femur 1.01, patella 0.37, tibia 0.66, metatarsus 0.53, tarsus 0.53 (incl. claws). Leg 4 femur 1.37, patella 0.33, tibia 0.82. Opisthosoma dimensions difficult to measure; scutum (length 1.67, width 1.59) on dorsal surface. Spinnerets not preserved.

Description of additional specimen NIGP148238 (Figs. 37, 38).—Juvenile? Carapace length ca 2.35, width 1.84. Chelicerae large, robust, with peg-teeth extending from distal edge down length of mesal edge; fang perpendicular to long axis of paturon; length 1.50. Pedipalps on both sides not bulbous, with thin spines; tarsus 0.56. Legs short; leg formula 1243. Podomere lengths: leg 1 femur 1.80, patella long 0.87, tibia 1.35, metatarsus 1.24, tarsus 0.87. Leg 2 femur 1.68, patella short 0.66, tibia 1.30, metatarsus ≥ 0.88. Leg 3 femur 0.96, patella 0.47, tibia 0.93, metatarsus 0.70, tarsus 0.58 (incl. claws). Leg 4 tibia 1.23, metatarsus 0.99, tarsus 0.61 (incl. claws). Opisthosoma length c. 3.23, width c. 2.79; scutum (length ≥ 1.00 width ≥ 0.96) on dorsal surface. Spinnerets not preserved.

Description of additional specimen NIGP148239a,b (Figs. 39, 40).—Juvenile? Carapace length 2.28, width 1.65, cephalic region width 1.12. Chelicerae large, robust; fang perpendicular to long axis of paturon; length 1.30. Pedipalps on both sides not bulbous; length ≥ 1.55, tibia 0.56, tarsus 0.60. Legs short; leg formula 1243. Podomere lengths: leg 1 femur 1.73, patella

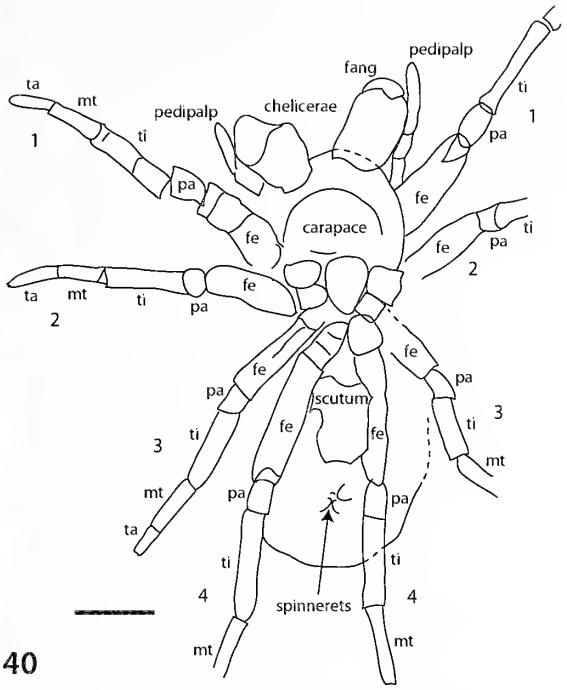


Figures 33–38.—*Sinaranea metaxyostraca* new genus and species. Juveniles? 33. Photograph of NIGP148236; 34. Camera lucida drawing of NIGP148236, explanatory drawing for Figure 33; 35. Photograph of NIGP148237; 36. Camera lucida drawing of NIGP148237, explanatory drawing for Figure 35; 37. Photograph of NIGP148238; 38, Camera lucida drawing of NIGP148238, explanatory drawing for Figure 37; Scale = 1.0 mm.

long 0.61, tibia 1.20, metatarsus 0.69, tarsus 0.56. Leg 2 femur 1.15, patella short 0.33, tibia 1.10, metatarsus 0.63, tarsus 0.50 (incl. claws). Leg 3 femur 1.15, patella 0.43, tibia 1.06, metatarsus 0.82, tarsus ≥ 0.32. Leg 4 femur 1.46, patella 0.45, tibia 1.61, metatarsus 0.93. Opisthosoma length 3.02, width 2.16; scutum (length ≥ 1.04 width ≥ 0.77) on dorsal surface. Spinnerets on ventral surface ca ¼ of length of opisthosoma from posterior.

DISCUSSION

The presence of palpimanoids, and especially archaeids, in strata of Jurassic age confirms the geological age of the Palpimanoidea, and the presence of identifiable palpimanoid families in the Jurassic suggests an even earlier origin for the superfamily. The presence of the group in the Jurassic of China is especially interesting because it extends the geo-



Figures 39, 40.—*Sinaranea metaxyostraca* new genus and species. Juvenile? 39. Photograph of NIGP148239a; 40. Camera lucida drawing of NIGP148239a, explanatory drawing for Figure 39; Scale = 1.0 mm.

graphic range of the superfamily. Today, spiders of the superfamily Palpimanoidea are widespread throughout tropical and subtropical areas of the world, but most constituent families have more limited distributions. Living archaeids are known from Australia, South Africa and Madagascar, a classic Gondwanan distribution. Fossil archaeids, however, are known from the Jurassic of Kazakhstan (Eskov 1987), China (this paper), the Cretaceous of Myanmar (Penney 2003), Baltic amber (Wunderlich 2004), and Madagascan copal (Lourenço 2000). The Kazakhstan and North China plates form a part of eastern Laurasia which had accreted by late Devonian times; the part of Myanmar which produces Cretaceous amber (Grimaldi et al. 2002) was situated on the Sibamisu terrane, which formed the northern shore of the Tethys ocean in the late Cretaceous (Metcalfe 2005). The origin of Baltic amber lies in western Laurasia. The presence of archaeids in the eastern Laurasian part of Pangaea in the Mesozoic and western Laurasia in the Cenozoic appears at first to eontradict the present-day Gondwanan distribution of the family. Archaeids are small, litter-inhabiting spiders, and their dispersal abilities are probably low. The present disjunct distribution of the family suggests a geological history that pre-dates the break-up of Gondwana in Jurassic times and the fossil occurrences suggests a cosmopolitan distribution in the Mesozoic. The lack of Mesozoic fossils in the Gondwana area can be explained by the rarity of suitable fossil sites there. The Cretaceous Myanmar archaeid was referred by Penney (2003) to the modern genus *Afrarchaea*, which today occurs in southern Africa. This genus must, therefore, have occurred from the northern shores of the Tethys Ocean down to the central Gondwana area at that time. Fossil evidence thus demonstrates that the present-day distribution of archaeids probably results from a reduction in the former range of the family (the theory of ousted relics: Eskov & Golovatch 1986; Eskov 1987, 1992), perhaps as a consequence of Neogene climate cooling (Grimaldi & Engel 2004).

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Estimating the diversity of arboreal oonopid spider assemblages (Araneae, Oonopidae) at Afrotropical sites

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Abstract. The abundance, species richness, and assemblage structure of arboreal Oonopidae of Afrotropical rainforests and savannahs was investigated. Canopy-dwelling spiders were collected by insecticide knockdown fogging at 11 rainforest and three savannah sites in West, Central, and East Africa. In two lowland rainforests (Luki, DR Congo, and Kakum, Ghana) and two savannahs (Faro, Cameroon, and Mkomazi, Tanzania) Oonopidae were the second most abundant spider family, comprising up to 22% of the arboreal arachnofauna. In total, 51 speeies and 11 genera of Oonopidae were recorded from the 14 study sites. Kakum was the most species- and genus-rich site, with 11 species and 5 genera recorded. The arboreal oonopid assemblages were almost invariably found to be dominated by the widely-distributed genera *Orchestina* Simon and *Opopaea* Simon, in terms of both abundance and species richness. *Orchestina* in particular can be highly abundant and can comprise more than 90% of arboreal oonopids in rainforests as well as in savannahs. Species accumulation curves and six nonparametric estimators of total species richness (Chao 1, Chao 2, ACE, first- and second-order jackknife, and bootstrap) were calculated for Luki, Kakum, and Faro to evaluate the level of inventory completeness. In Kakum and Faro the species accumulation curve respectively closely approached and reached a stable asymptote. The selected nonparametric estimators were found to lack predictive power when applied to the Faro data set and appeared to behave similarly poorly on the Kakum sample set.

Keywords: Goblin spiders, Planetary Biodiversity Inventory, rarefaction, tree crowns, ecology

The Oonopidae (goblin spiders) are a worldwide family of very small spiders whose diversity, phylogeny and ecology remain poorly known. In major spider compendia (e.g., Dippenaar-Schoeman & Jocqué 1997; Song et al. 1999; Ubick et al. 2005) and in papers on their taxonomy and biology (e.g., Saaristo & van Harten 2002; Burger 2007) oonopids are usually treated as being mainly restricted to the ground layer. Yet, this prevailing view on the vertical distribution of the family may be in need of revision as several canopy survey studies published since 1990 have demonstrated the presence of oonopids in the radically different environment of tropical forest canopies (Table 1 summarizes this literature). At some sites Oonopidae were even reported to constitute a major component of the arboreal arachnofauna in terms of abundance, accounting for up to 17% of all adult spiders collected (Sorensen 2004).

Despite the increasing number of reports, current knowledge of arboreal oonopid assemblages can still only be described as rudimentary since even primary, descriptive data is largely lacking. Perhaps most notable in this regard is the paucity of data on the morphological diversity of canopy-dwelling Oonopidae. Although a majority of the aforementioned studies have recorded species numbers, only two (Russell-Smith & Stork 1994, 1995) have provided genus-level identifications of the oonopid fauna.

In this study we present data on the abundance, species richness, and generic affinities of canopy-inhabiting Oonopidae at 14 Afrotropical rainforest and savannah sites. In addition, species accumulation curves and several nonparametric estimators are used to estimate total species richness of arboreal oonopid assemblages at three of these sites.

METHODS

Study sites.—Canopy spiders were collected by insecticide knockdown fogging at 14 sites in West, Central, and East Africa. Figures 1a–b show the location of all study sites. Details on the localities Luki, Kakum, and Faro are given below, while characteristics of the other study sites are listed in Table 2; additional information on Kakamega, Budongo, Cyamudongo, Ibanda Makera, Mkomazi, and Comoé can be found in Freund (2005), Wagner (1997, 2003), Krüger & McGavin (1997), and Mody et al. (2003).

Luki Biosphere Reserve (05°37′S, 13°06′E) is situated in the Bas-Congo region of the DR Congo and consists of lowland rainforest. Annual rainfall averages 1120 mm, with a single wet season usually lasting from mid-October to mid-May. Fog days average 164 per year. Five primary forest samples were taken at an elevation of about 266 m between 4 and 13 November 2006.

Kakum National Park (05°21′N, 01°23′W) is situated in the Central Region province of Ghana and consists of adjacent plots of primary and 40 year-old secondary rainforest. Rainfall averages 1500–1800 mm per year and is bimodal, with wet seasons between March–July and September–November. Twelve samples (six from primary and six from secondary forest canopy) were taken at an elevation of about 159 m between 12 and 25 November 2005.

Faro Game Reserve (08°24′N, 12°49′E) is located in northern Cameroon and consists of wooded savannah and gallery forest. Average annual rainfall is 500–1000 mm. Ten gallery forest trees and nine savannah trees were sampled at an elevation of about 300 m between 18 April and 3 May 2007, at the beginning of the local wet season (May–October).

Collecting methods.—We used the following fogging protocol in Luki, Kakum, and Faro. On each sampling occasion a SWINGFOG SN 50 fogger (Swingtec GmbH) was operated from the ground for 6 (Faro) or 10 (Luki, Kakum) minutes, generating an insecticidal fog from a 1% solution of natural pyrethrum in diesel. Arthropods were collected on triangular or rectangular sheets with a combined area of about 64 (Luki, Kakum) or 72 (Faro) square meters. Sheets were suspended

Table 1.—Overview of published data on the abundance and species richness of Oonopidae in tropical and subtropical forest canopies. * denotes studies that included juvenile spiders. Rank: rank of Oonopidae among all spider families present at a site.

Study site	Habitat	Total Spider Indivs.	Oonopidae Ind.	Oonopidae %	Oonopidae Rank	Total spider spp.	Oonopidae Spp.	Oonopidae %	Oonopidae Rank	Reference
Uzungwa, Tanzania	rainforest	5233	884	16.9	2/28	149	3	2.0	11/28	Sørensen 2004
Samiria River, Peru	rainforest	4068	394	9.7	5/37	844	30	3.6	7/37	Silva 1996
Tambopata-Candamo, Peru	rainforest	1427	73	5.1	6/30	673	34	5.1	6/30	Silva 1996
Reserva Adolpho Ducke, Brazil	rainforest	81	12	14.8	3/16	?	?	?	?	Höfer et al. 1994
Kinabalu/Crocker Range, Borneo	rainforest	6999	272	3.9	7/29	578	7	1.2	12/29	Floren & Deeleman-Reinhold 2005
Ladan Hills, Borneo	rainforest	945	23	2.4	9/22	190	4	2.1	7/22	Russell-Smith & Stork 1995*
Dumoga-Bone, Sulawesi	rainforest (lowland)	1211	46	3.8	8/19	?	?	?	?	Russell-Smith & Stork 1994*
Dumoga-Bone, Sulawesi	rainforest (submontane)	438	48	11.0	4/14	50	5	10.0	4/14	Russell-Smith & Stork 1994*
Mt. Glorious, Australia	rainforest	1408	8	0.6	8/19	72	2	2.8	7/19	Basset 1990, 1991
Mt. Nondoué, Païta, New Caledonia	sclerophyll forest	4947	188	3.8	5/11	?	?	?	?	Guilbert et al. 1994*
Pindaï, New Caledonia	sclerophyll forest	6768	512	7.6	4/17	?	?	?	?	Guilbert 1997*
Rivière Bleue, New Caledonia	rainforest	1594	78	4.9	4/17	?	?	?	?	Guilbert 1997*

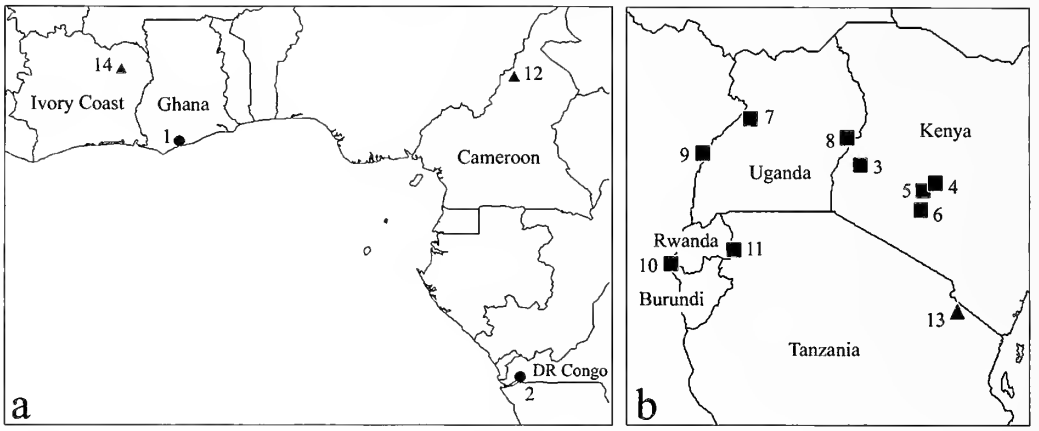
1.5 m above the ground. In Faro, individual trees were fogged while in Luki and Kakum selected areas (10–15 m high) of the closed canopy were targeted. After a drop time of 2 hours, specimens were concentrated by brushing and subsequently stored in 70% (Luki, Kakum) or absolute (Faro) ethanol. Sampling usually took place at dawn when wind speeds were lowest. In Luki the first fogging was disturbed by severe fog scatter. The same patch of canopy was refogged 18 hours later when weather conditions were more favorable. As these two foggings yielded a combined number of oonopids comparable to most undisturbed samplings, they were merged and counted as a single sample (first sample in the species-by-sample matrix, see below). Understorey vegetation was avoided or, when possible, cleared. The other 11 sites were sampled by W. Freund (Kakamega), G. McGavin (Mkomazi), K. Mody (Comoé), and T. Wagner (Kakamega, Mt Kenya, Aberdare, Gatamayu, Budongo, Mt. Elgon, Semliki, Cyamudongo, and Ibanda Makera) between October 1993 and January 2003. Details on the fogging protocols used at these sites can be found in the references given in Table 2.

Morphotyping.—All adult spiders collected were identified to family level and sorted to morphospecies. Subsequently, the generic affinities of all oonopid morphospecies were determined. When morphospecies could not be accommodated in one of the 73 currently described genera (Platnick 2008) they were assigned to morphogenera coded undescribed genus 1, 2, 3 etc. In order not to artificially inflate species and genus counts, a conservative approach was applied to delimiting morphospecies and morphogenera (henceforth referred to as species and genera). The material is deposited in the Royal Museum for Central Africa in Tervuren, Belgium (Luki, Kakum, and Faro), the Oxford University Museum of Natural History in Oxford, UK (Mkomazi), and the Alexander Koenig Museum in Bonn, Germany (other sites).

Comparison of subhabitats.—In both Kakum and Faro two distinct subhabitats were sampled. A two-sample t-test was applied to the Kakum data to check for differences in oonopid abundance and species richness between primary and seeondary forests. Hierarchical cluster analyses were then performed to evaluate whether these forest types differed markedly in community composition. First, we calculated four different indices of compositional similarity viz. the incidence (presence/absence)-based classic Jaccard and Sorensen indices and the abundance-based Bray-Curtis and Morisita-Horn indices. Four dendrograms were subsequently generated from each similarity matrix by implementing four different joining algorithms viz. single linkage (nearest neighbor), complete linkage (furthest neighbor), centroid linkage, and Ward's method. The 16 resulting dendrograms were then inspected to assess the level of clustering among samples from the same forest type.

As data deviated significantly from normality (Shapiro-Wilk test, $P < 0.01$), the nonparametric Mann-Whitney U statistic was used to test for significant differences in oonopid abundance between gallery forest and savannah trees at Faro. Differences in species richness and community composition were evaluated as outlined above.

The comparisons between subhabitats constitute comparative mensurative experiments (Hurlbert 1984). In order to reduce the risk of pseudoreplication sensu Hurlbert (1984) we



Figures 1a, b.—Location of study sites. a. Kakum (1), Luki (2), Faro (12) and Comoé (14); b. Kakamega (3), Mt. Kenya (4), Aberdare (5), Gatamayu (6), Budongo (7), Mt. Elgon (8), Semliki (9), Cyamudongo (10), Ibanda Makera (11) and Mkomazi (13). ● lowland rainforest ■ montane forest ▲ savannah.

selected trees (or areas of canopy) that were dispersed throughout the subhabitat. A single sample was taken from each tree or area of canopy.

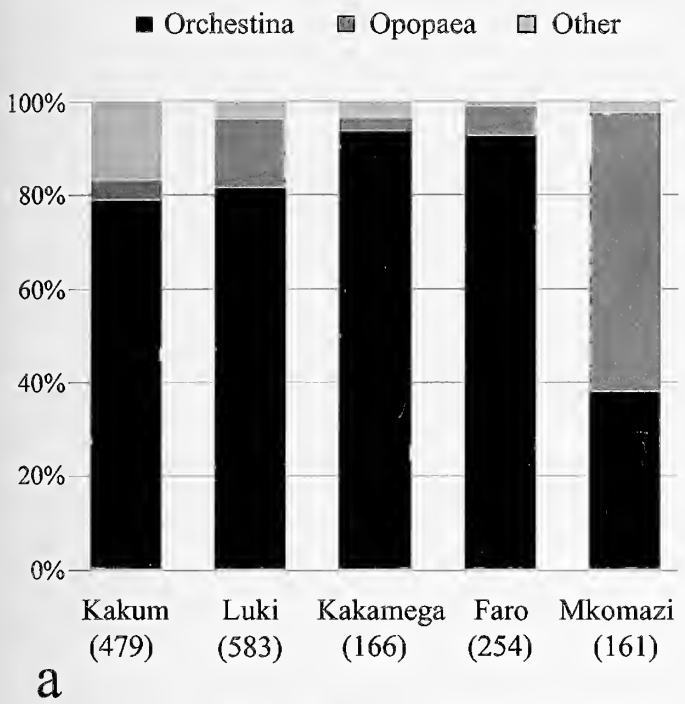
Total oonopid species richness.—For Luki, Kakum, and Faro the exact composition of each individual sample taken is known. This allowed us to estimate the total oonopid species richness at these sites and to evaluate the completeness of our censuses. For this purpose species accumulation curves (also called sample-based rarefaction curves, Gotelli & Colwell 2001) were calculated analytically ("Mao Tau," Colwell et al.

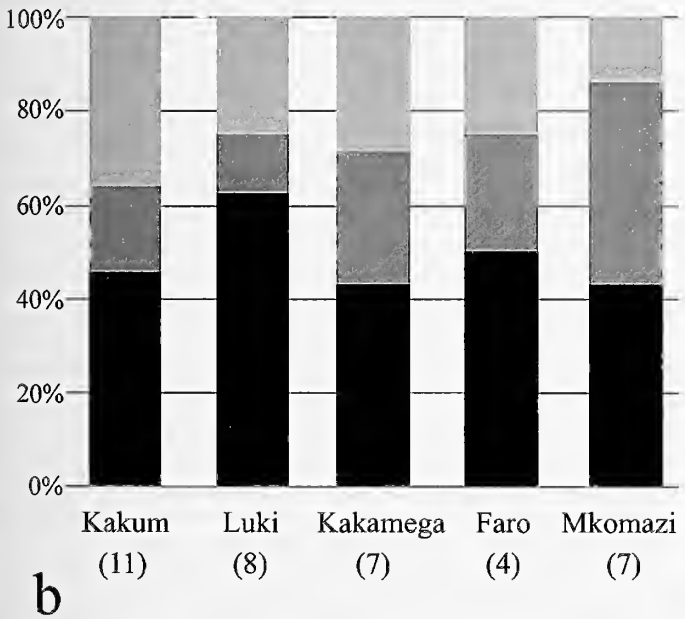
Table 2.—Habitat and sampling details for 11 of the 14 study sites (see Methods section for details on Luki, Kakum, and Faro).

		Sampling		
Study site	Habitat	No. of samples	Season	Fogging protocol
Kakamega Forest, Kenya	prim./sec. forest	200	wet/dry	Wagner 2003, Freund 2005
Mt. Kenya, Kenya	prim. rainforest	19	dry	Wagner 2003
Aberdare, Kenya	prim. rainforest	8	dry	Wagner 2003
Gatamayu, Kenya	prim. rainforest	23	dry	Wagner 2003
Budongo Forest, Uganda	prim./swamp/sec. forest	103	wet/dry	Wagner 2003
Mt. Elgon, Uganda	prim. rainforest	8	dry	Wagner 2003
Semliki Forest, Uganda	prim. rainforest	24	dry	Wagner 2003
Cyamudongo, Rwanda	sec. rainforest	9	wet	Wagner 1997
Ibanda Makera, Rwanda	gallery/dry forest	7	wet	Wagner 1997
Mkomazi, Tanzania	semiarid savannah	31	dry	Krüger & McGavin 1997
Comoé, Ivory Coast	Guinea-savannah	31	wet	Mody et al. 2003

Table 3.—Abundance and species richness of arboreal Oonopidae at 14 Afrotropical rainforest (lowland and montane) and savannah sites. s %: percentage of singletons. Rank: rank of Oonopidae among all spider families present at a site.

		Total spider	Oonopidae			Total spider	Oonopidae			
Study site	Habitat	indivs.	Ind.	%	Rank	spp.	Spp.	%	Rank	s %
Kakum, Ghana	lowland	4587	479	10.4	2/27	297	11	3.7	6/27	9.1
Luki, DR Congo	lowland	3545	583	16.4	2/26	231	8	3.5	8/26	12.5
Kakamega, Kenya	montane	3452	166	4.8	6/29	367	7	1.9	9/29	28.6
Mt. Kenya, Kenya	montane	1957	60	3.1	5/21	85	7	8.0	4/21	14.3
Aberdare, Kenya	montane	1136	15	1.3	9/16	42	4	9.5	4/16	25
Gatamayu, Kenya	montane	1082	65	6.0	4/20	79	4	5.1	5/20	0
Budongo, Uganda	montane	2844	89	3.1	7/24	422	7	1.7	9/24	14.3
Mt. Elgon, Uganda	montane	2516	137	5.4	3/13	33	3	9.1	3/13	0
Semliki, Uganda	montane	276	29	10.5	3/16	122	3	2.5	8/16	33.3
Cyamudongo, Rwanda	montane	198	9	4.5	6/16	67	2	3.0	7/16	0
Ibanda Makera, Rwanda	montane	117	4	3.4	8/12	54	2	3.7	7/12	50
Faro, Cameroon	savannah	1162	254	21.9	2/18	96	4	4.2	6/18	0
Mkomazi, Tanzania	savannah	1078	161	14.9	2/18	196	7	3.6	6/18	14.3
Comoé, Ivory Coast	savannah	764	12	1.6	9/17	125	1	0.8	12/17	0





Figures 2a, b.—Relative abundance and species richness of *Orchestina*, *Opopaea*, and other genera at the five study sites where >150 Oonopidae were collected. a. Relative abundance (total oonopid abundance is given in brackets for each site); b. Relative species richness (observed oonopid species richness in brackets).

2004). In addition, six nonparametric richness estimators were plotted using 200 randomizations (without replacement) of sample accumulation order. Nonparametric estimators assess "true" richness from the distribution of rare or infrequent species and are considered the most promising and potentially most powerful approach to estimating the total species richness of communities (Gotelli & Colwell 2001; Magurran 2004), usually outperforming other methods such as curve-

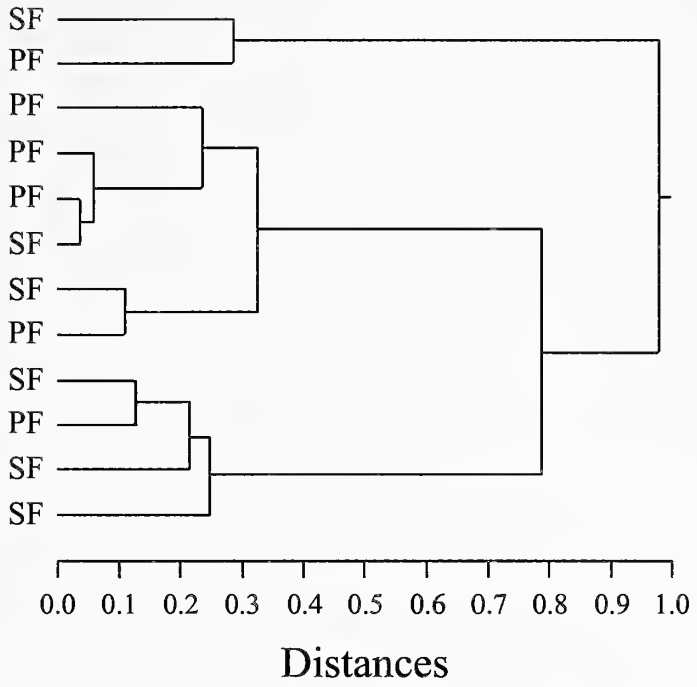


Figure 3.—Dendrogram (Morisita-Horn index/complete linkage) of primary forest (PF) and secondary forest (SF) samples taken at Kakum.

fitting (Walther & Moore 2005). The estimators selected were the abundance-based Chao 1 and ACE and the incidence-based Chao 2, bootstrap and first- and second-order jackknife (henceforth Jack 1 and Jack 2). The bias-corrected forms of Chao 1 and 2 were used. Because the collecting protocol applied in Luki, Kakum, and Faro resulted in large but relatively few samples the ICE estimator was not selected. The Coleman-curve was also calculated for each site. Computation of individual-based rarefaction curves such as the Coleman-curve assumes random mixing of individuals and the difference between a species accumulation curve and the corresponding Coleman-curve therefore serves as a measure of patchiness (Colwell & Coddington 1994).

Similarity indices, rarefaction curves and estimators were calculated using EstimateS version 8.0.0 (Colwell 2006). SYSTAT version 12 was used for statistical analyses and hierarchical clustering. Further details on rarefaction curves and on the similarity indices and nonparametric estimators used in this study are provided by Gotelli & Colwell (2001), Magurran (2004) and on the EstimateS website (Colwell 2006). Species-by-sample abundance matrices for Luki, Kakum, and Faro are available online at http://www.africamuseum.be/research/zoology/invertebrates/index_html in EstimateS Format 1.

RESULTS

Abundance and diversity of arboreal Oonopidae.—Our data on the relative importance of Oonopidae as a component of arboreal spider faunas are presented in Table 3. In both lowland rainforests oonopids rank second in abundance only to the Theridiidae, accounting for 10.4% in Kakum and 16.4% in Luki. In two out of three investigated savannah sites, oonopids also rank second in terms of abundance (in both

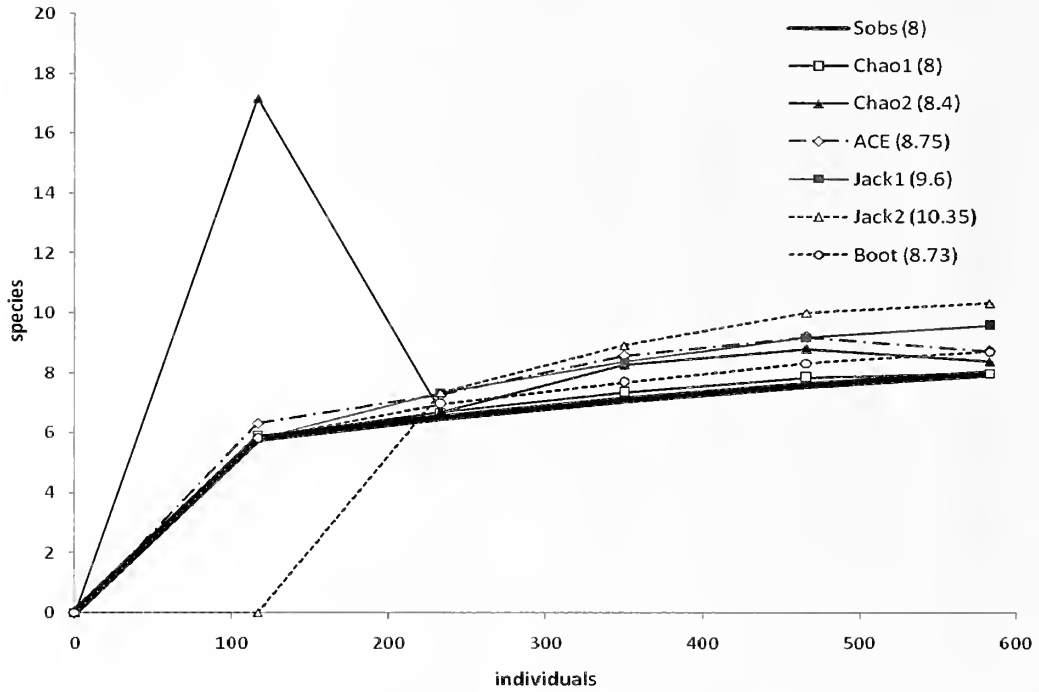


Figure 4.—Species accumulation curve (Sobs) and nonparametric estimator curves for Luki. Final values in brackets. Boot = bootstrap.

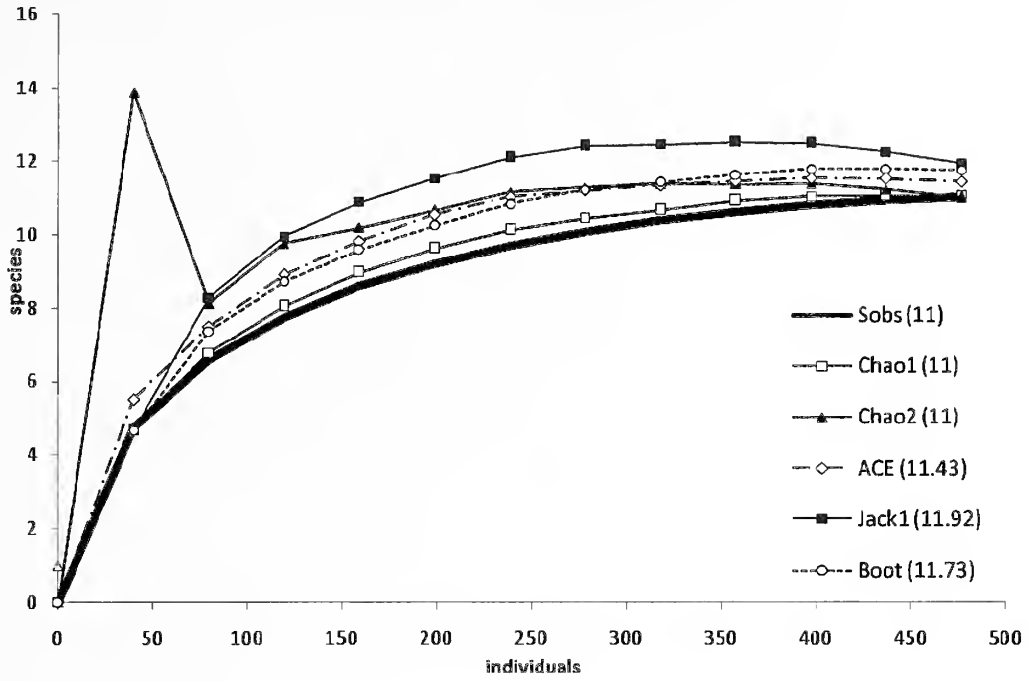
cases again after theridiids), contributing 14.9% in Mkomazi and 21.9% in Faro. Oonopidae usually comprise a small proportion of total spider species richness but they do contribute substantially (more than 9%) to the relatively species-poor arboreal arachnofaunas of some montane forests (Aberdare, Mt. Elgon). The lowland rainforest of Kakum emerges as the most speciose and genus-rich site, with 11 species and 5 genera of Oonopidae observed. Species richness in savannah habitats varies from low (only 1 species in Comoé despite considerable sampling efforts, see Mody et al. 2003) to relatively high (seven species in Mkomazi, equalling or exceeding the observed richness in most investigated rainforest sites). The relatively low proportion of species represented by a single individual (singletons; Table 3) can be taken as an indication that the arboreal oonopid assemblages have been sampled representatively at most study sites.

The 2063 adult Oonopidae collected from the 14 study sites belong to 51 species and 11 genera. A high proportion of the inventoried genera (73%) are presently undescribed. The genus *Opopaea* Simon 1891 was recorded in all sites while *Orchestina* Simon 1882 occurred in seven rainforest and two savannah sites. Most other genera were recorded from only one or two sites (Appendix 1 gives a complete overview of the species collected at each site). Of the total number of collected oonopids *Orchestina* makes up 67.4% and *Opopaea* 22.8%. All other genera contribute very little, with undescribed genus 4 being the most abundant (3.7%). *Orchestina* and *Opopaea* comprise 35.3% and 33.3%, respectively, of the total number of recorded species, with undescribed genus 1 ranking third (7.8%). The dominance of *Orchestina* and *Opopaea* also holds when individual study sites are considered, as these two genera account for most of the oonopid abundance and species richness at almost every site (Figs. 2a, b). *Orchestina* in particular can be highly dominant, as exemplified by the study sites Luki, Kakum, Kakamega, and Faro (Fig. 2a).

Comparison of subhabitats.—In Kakum, primary and secondary forest samples did not differ significantly in oonopid abundance (t-test, $P = 0.85$) or species richness (t-test, $P = 0.88$). The 16 dendrograms that were generated exhibited considerable differences in topology. However, primary and secondary forest samples did not form separate clusters within any of these trees but instead were almost completely interspersed throughout each dendrogram (Fig. 3). A similar lack of differentiation between primary and secondary forest assemblages was found in most other spider families present in Kakum (own unpublished data) and may arise primarily from the close adjacency of both forest types, which permits ready recolonization of the regenerating secondary forest.

Gallery forest trees and savannah trees in Faro did neither differ signifieantly in abundance (Mann-Whitney test, $P = 0.65$) nor in species richness (t-test, $P = 0.79$). As in Kakum, the cluster analysis dendrograms lacked any resolution for subhabitat type. Both the Faro and Kakum data sets are, therefore, analyzed as a whole in the following section.

Estimation of total oonopid species richness.—In Luki (eight observed species; Fig. 4) the species accumulation curve continues to rise as sample number increases without showing signs of approaching an asymptote. The Chao 1 estimator curve closely resembles the empirical curve but appears to level off at high sample numbers. ACE and Chao 2 estimates begin to fall as the maximum number of samples is approached. The Jack 1, Jack 2, and bootstrap curves on the other hand, continue to rise in parallel with the species accumulation curve. This lack of consensus among estimators is echoed in their total richness estimates, which do not cluster tightly but range from 8 (for Chao 1) to 10.35 (Jack 2). Taken together, these results do not provide clear evidence that the inventory at Luki was nearing completeness and sustained collecting efforts may therefore result in many as yet unseen species.



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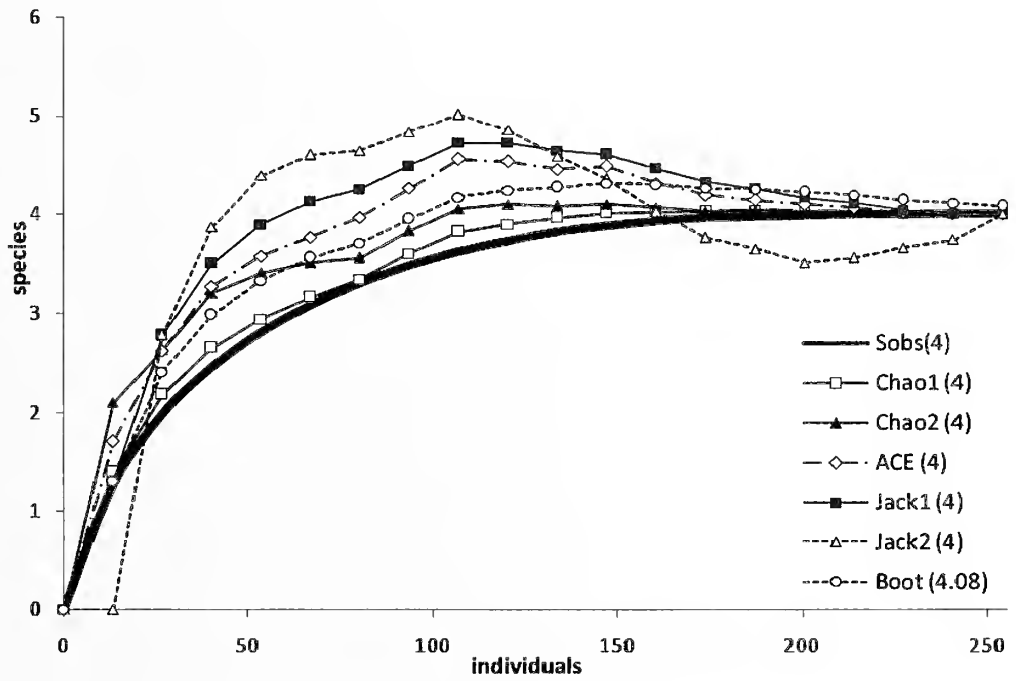

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Figures 5a, b.—Species accumulation curves (Sobs) and nonparametric estimator curves for Kakum and Faro. a. Kakum; b. Faro. Final values in brackets. Boot = bootstrap.

In Kakum (11 observed species; Fig. 5a), the species accumulation curve approaches a stable asymptote as the maximum number of samples is reached. Of the estimators tested, only Jack 2 fails to provide a reasonable estimate as it generates a total species richness estimate (10.48) that is lower than the observed number of species (see Sørensen 2004 for another example of this behavior); it is therefore not presented in Figure 5a. All other estimator curves start to decline as the maximum number of samples is approached and finally converge closely on the observed richness, with estimates ranging from 11 (for Chao 1 and Chao 2) to 11.92 (for Jack 1).

In Faro (four observed species; Fig. 5b) the species accumulation curve reaches a stable asymptote. This condition eliminates the need for nonparametric estimators but at the same time allows for a direct and rigorous test of their performance (Gotelli & Colwell 2001). As in Kakum, the Jack 2 estimator performs least satisfactorily, generating an erratic curve which is still climbing steeply at its end point. The other

estimator curves level off as increasingly more samples are pooled and finally stabilize at an estimate of 4 species, with the exception of the bootstrap curve which continues to decline slowly and gives a final estimate of 4.08. However, none of the estimators stabilizes sooner than the species accumulation curve.

No evidence for a strong departure from the assumption of homogeneity (Colwell & Coddington 1994) was found, the species accumulation curves lying at most 0.25 (Luki), 1.01 (Faro), and 2.15 (Kakum) standard deviations (SDs) below their corresponding Coleman-curves (for comparison, the seed bank data set of Colwell & Coddington (1994) gives a maximum difference of 1.7 SDs). The near-identity of the empirical and Coleman-curves in Luki indicates a very low level of patchiness.

DISCUSSION

The first quantitative data on arboreal Oonopidae of the Afrotropical region were provided by Sorensen (2004), who reported that oonopids accounted for almost 17% of the canopy spiders in a Tanzanian montane forest. In the present study, similarly high abundances are recorded from lowland rainforests and even from savannahs. Furthermore, it is shown that arboreal oonopid assemblages can be both speciose and genus-rich. Despite their often considerable morphological diversity, assemblages were invariably found to be dominated by either *Opopaea* or *Orchestina*. The dominance of the latter genus, in particular, can be very pronounced and is not geographically restricted to the African tropics, as *Orchestina* also dominates canopy-dwelling oonopid faunas on Borneo (C. Deeleman, pers. comm.) and Sulawesi (A. Russell-Smith, pers. comm.).

Calculation of species accumulation curves showed that our inventory at Faro was essentially complete and the 4 species and 3 genera collected at this savannah site thus very likely represent the entire oonopid fauna that is accessible to the fogging method and present as adults at the beginning of the rainy season. Similarly, the 11 species and 5 genera collected at Kakum were shown to represent a nearly complete inventory of the arboreal oonopid assemblage of this lowland rainforest.

Although the selected nonparametric estimators all converged very closely on the observed richness when applied to the Faro data set, none reached a stable asymptote sooner than the species accumulation curve (one of the most desirable properties of a good estimator, Gotelli & Colwell 2001) and all estimators were thus devoid of any predictive power. When judged against this asymptote criterion, the estimators also seem to perform poorly on the Kakum sample set, as none of the plotted estimator curves appears to approach an asymptote much faster than the empirical curve.

As a consequence of our and Sørensen's surveys in Africa, assemblage structure is now better known for canopy-dwelling Oonopidae than for their ground-living counterparts, a rather unusual state of affairs for a tropical spider family. Yet, many important questions remain to be addressed. One of these concerns the extent of seasonal changes in arboreal oonopid assemblages. These may be considerable, as indicated by the large seasonal fluctuations in oonopid abundance recorded in two New Caledonian forests (E. Guilbert, pers. comm.). Perhaps most urgently needed, however, are studies that investigate the level of vertical stratification of oonopid communities by comparing the canopy- and ground-dwelling faunas of a single site with regard to their species composition. Recent pitfall trapping in primary forest in Luki (November 2006 and September-October 2007) suggests that oonopid communities can be strongly vertically stratified, as only one of the seven species collected at ground-level also occurs in the canopy (own unpublished data). The knowledge gained by studies addressing vertical stratification and seasonal variation can in turn be used to manage collection resources for the ongoing Planetary Biodiversity Inventory project on this spider family (www.research.amnh.org/oonopidae).

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Appendix 1.—Number of individuals per species at each site.

	Kakum, Ghana	Luki, DR Congo	Kakamega, Kenya	Mt. Kenya, Kenya	Aberdare, Kenya	Gatamayu, Kenya	Budongo, Uganda	Mt. Elgon, Uganda	Semliki, Uganda	Cyamudongo, Rwanda	Ibanda Makera, Rwanda	Faro, Cameroon	Mkomazi, Tanzania	Comoé, Ivory Coast	**Total**
Ischnothyreus sp.1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	**1**
Opopaea sp.1	15	-	-	-	-	-	-	-	-	-	-	-	-	-	**15**
Opopaea sp.2	6	-	-	-	-	-	-	-	-	-	-	-	-	-	**6**
Opopaea sp.3	-	86	-	-	-	-	-	-	-	-	-	-	-	-	**86**
Opopaea sp.4	-	-	-	18	4	17	-	78	-	-	-	-	-	-	**117**
Opopaea sp.5	-	-	2	-	-	-	13	-	26	-	3	-	-	-	**44**
Opopaea sp.6	-	-	-	-	-	-	-	-	1	-	-	-	-	-	**1**
Opopaea sp.7	-	-	-	-	-	-	-	-	-	7	-	-	-	-	**7**
Opopaea sp.8	-	-	-	-	-	-	-	-	-	-	-	16	-	12	**28**
Opopaea sp.9	-	-	3	-	-	-	-	-	-	-	-	-	-	-	**3**
Opopaea sp.10	-	-	-	-	-	28	-	-	-	-	-	-	-	-	**28**
Opopaea sp.11	-	-	-	-	1	6	-	-	-	-	-	-	-	-	**7**
Opopaea sp.12	-	-	-	12	7	-	-	-	-	-	-	-	-	-	**19**
Opopaea sp.13	-	-	-	6	-	-	-	-	-	-	-	-	-	-	**6**
Opopaea sp.14	-	-	-	7	-	-	-	-	-	-	-	-	-	-	**7**
Opopaea sp.15	-	-	-	-	-	-	-	-	-	-	-	-	70	-	**70**
Opopaea sp.16	-	-	-	-	-	-	-	-	-	-	-	-	25	-	**25**
Opopaea sp.17	-	-	-	-	-	-	-	-	-	-	-	-	1	-	**1**
Orchestina sp.1	134	-	-	-	-	-	-	-	-	-	-	-	-	-	**134**
Orchestina sp.2	91	-	-	-	-	-	-	-	-	-	-	-	-	-	**91**
Orchestina sp.3	138	308	82	-	-	-	25	-	-	-	-	-	-	-	**553**
Orchestina sp.4	7	-	-	-	-	-	-	-	-	-	-	-	-	-	**7**
Orchestina sp.5	-	19	-	-	-	-	-	-	-	-	-	-	-	-	**19**
Orchestina sp.6	-	2	-	-	-	-	-	-	-	-	-	-	-	-	**2**
Orchestina sp.7	-	2	-	-	-	-	-	-	-	-	-	-	-	-	**2**
Orchestina sp.8	7	142	1	-	-	-	19	-	-	-	-	-	-	-	**169**
Orchestina sp.9	-	-	72	-	-	-	-	-	-	2	-	-	-	-	**74**
Orchestina sp.10	-	-	-	-	-	-	20	-	-	-	-	-	-	-	**20**
Orchestina sp.11	-	-	-	-	-	-	5	-	-	-	-	-	-	-	**5**
Orchestina sp.12	-	-	-	-	-	-	1	-	-	-	-	-	-	-	**1**
Orchestina sp.13	-	-	-	4	-	14	-	-	-	-	-	-	-	-	**18**
Orchestina sp.14	-	-	-	-	-	-	-	-	-	-	-	-	10	-	**10**
Orchestina sp.15	-	-	-	-	-	-	-	-	-	-	-	-	45	-	**45**
Orchestina sp.16	-	-	-	-	-	-	-	-	-	-	-	-	6	-	**6**
Orchestina sp.17	-	-	-	-	-	-	-	-	-	-	-	228	-	-	**228**
Orchestina sp.18	-	-	-	-	-	-	-	-	-	-	-	7	-	-	**7**
Undescr. genus1 sp.1	-	-	-	-	-	-	-	16	-	-	-	-	-	-	**16**
Undescr. genus1 sp.2	-	-	-	-	-	-	-	-	2	-	-	-	-	-	**2**
Undescr. genus1 sp.3	-	-	1	-	-	-	6	-	-	-	-	-	-	-	**7**
Undescr. genus1 sp.4	-	-	-	12	3	-	-	-	-	-	-	-	-	-	**15**
Undescr. genus2 sp.1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	**1**
Undescr. genus3 sp.1	-	-	-	-	-	-	-	43	-	-	-	-	-	-	**43**
Undescr. genus3 sp.2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	**1**
Undescr. genus4 sp.1	52	-	-	-	-	-	-	-	-	-	-	-	-	-	**52**
Undescr. genus4 sp.2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**
Undescr. genus4 sp.3	-	23	-	-	-	-	-	-	-	-	-	-	-	-	**23**
Undescr. genus5 sp.1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	**2**
Undescr. genus6 sp.1	-	-	5	-	-	-	-	-	-	-	-	-	-	-	**5**
Undescr. genus6 sp.2	-	-	-	-	-	-	-	-	-	-	-	-	4	-	**4**
Undescr. genus7 sp.1	-	-	-	-	-	-	-	-	-	-	-	3	-	-	**3**
Undescr. genus8 sp.1	26	-	-	-	-	-	-	-	-	-	-	-	-	-	**26**
Total ind.	**479**	**583**	**166**	**60**	**15**	**65**	**89**	**137**	**29**	**9**	**4**	**254**	**161**	**12**	**2063**
No. of species	**11**	**8**	**7**	**7**	**4**	**4**	**7**	**3**	**3**	**2**	**2**	**4**	**7**	**1**	**51**
No. of genera	**5**	**4**	**4**	**4**	**2**	**2**	**3**	**3**	**2**	**2**	**2**	**3**	**3**	**1**	**11**

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Mating behavior of *Sickius longibulbi* (Araneae, Theraphosidae, Ischnocolinae), a spider that lacks spermathecae

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Abstract. We describe the mating behavior in the spermatheca-lacking theraphosid species *Sickius longibulbi* Soares & Camargo 1948. The behavior in captivity of nine pairs of *S. longibulbi* was videotaped and analyzed. The mating of this species presented an uncommon theraphosid pattern. There is little in the way of overt courtship by the male, the primary behavior seen being the male's use of legs I and II to touch the female's first pairs of legs and her chelicerae. Sometimes the male clasped one of the female's first pairs of legs, bringing her close to him. While the female raised her body, the male clasped her fangs and held her tightly with his legs III wrapped around her prosoma. The male seemed to try to knock the female down, pushing her entire body until she lay on her dorsum. In this phase we observed the male biting the female on the sternum or on the leg joints. When the female fell, the male attempted to position himself at an angle of 90° from the female. These movements appear to demand a lot of energy, particularly because the female is not passive during the mating. Our findings suggest that copulating in this position is, for the male, more successful than adopting other positions because it allows his extremely long palpal bulbs to deposit more sperm in the female oviduct where - since she lacks spermathecae - she retains the sperm. We suggest that the further he reaches into the oviduct, the greater the chance that he will fertilize the female's eggs.

Keywords: Mating behavior, reproductive success, tarantula, courtship, copulation

The family Theraphosidae is widespread in tropical and subtropical regions of the world, but the biology of theraphosid spiders is poorly known. Studies on the mating behavior of this family have been limited to a few species, namely *Dugesiella hentzi*, [now *Aphonopelma hentzi* (Girard 1852)] (Petrunkevitch 1911); *Eurypelma californicum* (Ausserer 1871) (now considered *nomen dubium*) (Baerg 1928); *Plesiopelma longisternale* (Schiapelli & Gerschman 1942) (Costa & Pérez-Miles 1992, 2002); *Aphonopelma chalcodes* Chamberlin 1940 (Minch 1979); *Brachypelma klaasi* (Schmidt & Krause 1994) (Yáñez et al. 1999); *Aphonopelma* sp. (Shillington & Verrell 1997); *Oligoxystre argentinense* (Mello-Leitão 1941) (now *Catumiri uruguayense* Guadanucci 2004); *Grammostola mollicoma* (Ausserer 1875); *Homoeomma uruguayense* (Mello-Leitão 1946); *Acanthoscurria suina* Pocock 1903; *Eupalaestrus weijenbergli* (Thorell 1894) (Costa & Pérez-Miles 2002); and *Xenodendrophila gabrielli* Gallon 2003 (now *Encyocratella olivacea* Strand 1907) (Kumar 2004). A prevalent pattern emerges from the available literature on theraphosid mating: courtship typically entails the male performing body vibrations and palpal drumming, with this being followed by clasping (i.e., to hook female's fangs or some appendage with the male tibial apophysis). In studies so far, mating always occurs with the male positioned in front of the female, with the male raising the female's body, allowing the male to reach the genital opening with his embolus.

Here we describe an unusual mating behavior in Theraphosidae, found in the species *Sickius longibulbi* Soares & Camargo 1948. This small Brazilian theraphosid is remarkable because of the absence of spermathecae, being the first Mygalomorphae species described to have this feature (Bertani & Silva, Jr. 2002).

Adults and juveniles of *S. longibulbi* were collected during a faunal rescue upstream of the dams of U.H.E. Sérgio Motta [21°32′ S, 52°05′ W] in the states of Mato Grosso do Sul and São Paulo, Brazil, in 2000. These are small theraphosids measuring about 20 millimeters in total body length (including chelicerae and excluding spinnerets) in both males and females. Voucher specimens from this study were deposited in the collection of the Laboratório de Artrópodes, Instituto Butantan, Brazil. The specimens were maintained separately in the laboratory in individual plastic cages with wet cotton wool and fed regularly with beetle larvae (*Tenebrio* sp.) and crickets (*Grillus* sp.).

Nine matings were recorded between 2000 and 2003. The male was introduced either into the female's cage (90 millimeters in diameter covered with soil: pairs 1 and 4 in Table 1); or both were introduced simultaneously into an arena floor of 450 × 360 mm covered with soil (Pairs 2, 3, 5, 6, 7, 8 in Table 1); at room temperature, in the morning or the afternoon. In one case, (pair 9 in Table 1), the female was placed two weeks before the mating encounter in a cage with soil of 300 × 300 × 150 mm of length / width / depth. She constructed a retreat under a Petri dish, allowing us to see her behavior inside it. All encounters were videotaped using a Handycam Sony TRV 15.

Since the females lack spermathecae, it is difficult to determine if they are adults. Consequently, in our experiments

Table 1.—Behavioral summary of the nine observed matings of *Sickius longibulbi*. Total = Percentage of individuals that exhibited each behavior at least once. F = male introduced in female's cage (90 mm in diameter covered with soil). A = male and female introduced simultaneously into an arena floor (450 × 360 mm covered with soil). R = male introduced in female's cage that constructed a retreat (300 × 300 × 150 mm covered with soil).

Pair	Courtship (male)	Courtship (female)	Male hug	Male bit	Male pushing (attempts)	Male pushing (success)	Male balance (attempts)	Palpal insertions on 90°	Mating in an angle close to 90°	Mating in usual theraphosid position	Mating duration (min)	Encounter
1	No	No	3	1	4	3	2	0	1	5	45	F
2	No	No	1	1	3	1	0	0	0	3	5	A
3	No	No	1	1	7	3	13	0	7	0	13	A
4	No	No	1	1	1	1	3	1	2	0	6	F
5	No	No	1	0	1	0	0	0	0	1	3	A
6	No	No	1	2	2	1	0	0	0	1	5	A
7	Yes	No	1	1	4	3	2	1	0	3	13	A
8	No	No	1	2	3	3	0	0	0	1	22	A
9	Yes	Yes	1	2	3	2	1	0	0	1	10	R
Total	22%	11%	100%	88%	100%	88%	55%	22%	33%	77%	3 to 45	

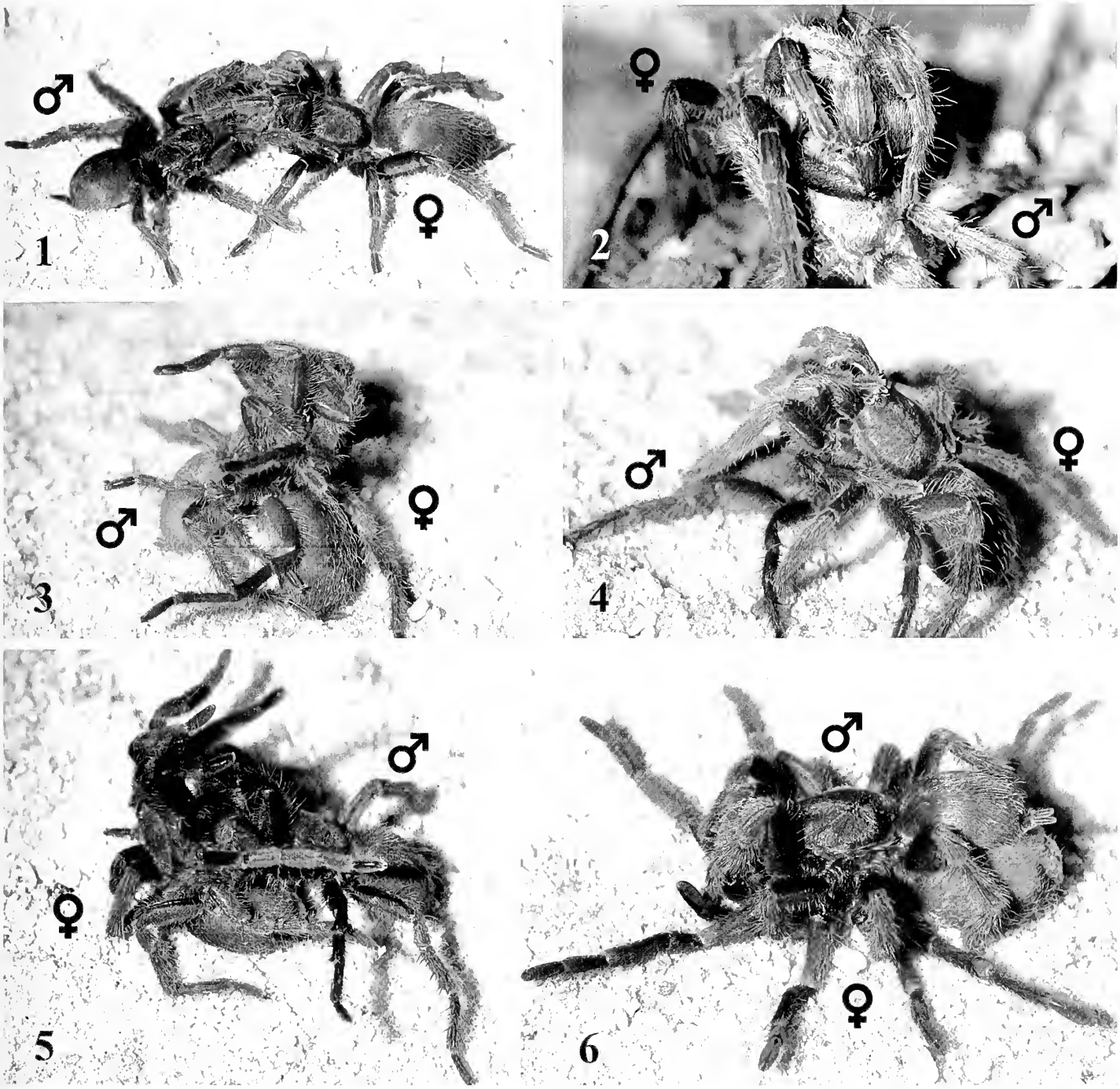
we used only the larger females and only if they did not have eggsacs. As the specimens came from the wild, it was not possible to determine if the females used in the experiments already had sperm inside them, since they are able to keep male sperm even after some molts (Bertani & Silva, Jr. 2002).

There was a common pattern when *S. longibulbi* mated (Figs. 1–9, Table 1). First, the male approached the female, touching the substrate with his legs I and II with very fast movements. He also moved his third legs and scratched his palps against the substrate. Then, the male touched the female with his legs I and II on her first pairs of legs and on the chelicerae (Fig. 1). The male sometimes clasped one of the female's first pair of legs, using his leg I tibial apophysis and a leg I metatarsal ventral apophysis (see figs. 4, 5 of Bertani & Silva, Jr. 2002; see also Fig. 11). The tibial apophysis was hooked on the female leg and then the curved metatarsus I was flexed catching the female leg (Fig. 12) and bringing her close to him. The curvature of metatarsus I, the incrassate tibia I, and the presence of an apophysis on the ventral metatarsus I are characteristics found in *Sickius longibulbi*, as well as *Porrhothele antipodiana* (Hexathelidae) (Jackson & Pollard 1990) and *Fufius* spp. (Cyrtaucheniidae) (pers. obs.). *Euagrus* spp. (Dipluridae) has similar structures on leg II (Coyle 1986). These structures are similar in form and function; i.e., used to clasp legs or palps, though the clasped appendages vary: in *Euagrus* the male clasps the female's femur II (Coyle 1986) and in *Porrhothele* he clasps the female's palpus (Jackson & Pollard 1990).

In *S. longibulbi*, when the female raised her body, the male clasped onto her fangs using the tibial apophyses (Fig. 2), and held her tightly with legs III around her prosoma (we call this behavior "hug") (Fig. 3). Subsequently, the male touched the female's posterior legs with his legs III many times (Fig. 4), appearing to be trying to knock her down, pushing and making her fall (the "male pushing attempts" and "male pushing success" in Table 1). In this phase we observed *Sickius longibulbi* males also moving their fangs many times, raising and lowering them near the female's sternum. Often, the male bit the female on the sternum or on the leg joints ("bite"; Table 1) and it was possible to see hemolymph droplets on the bitten region. Sometimes, the pair was in the usual position when the male suddenly pushed the female in a very fast movement (Fig. 5). This is a critical phase and the male was not always successful (Table 1). When the male succeeded, the female ended up lying on her dorsum, with the male over her, holding her tightly (Fig. 6). Subsequently, the male seemed to try to balance himself angled up at 90° to the female's horizontal body axis (the "balance" in Table 1) (Figs. 7–8). In this position the male inserted his long, slender embolus into the female genital opening (Fig. 9). Afterwards the male fell laterally, unclasping and moving away from the female.

Palpal insertions into the female's genital opening were difficult to see but seemed to occur with the spiders in the usual theraphosid copulatory posture. However, sometimes insertion was with the female lying on her back and the male in an angle approximately 90° in relation to the female axis (Table 1). In this position, however, it could be easily seen (Fig. 9).

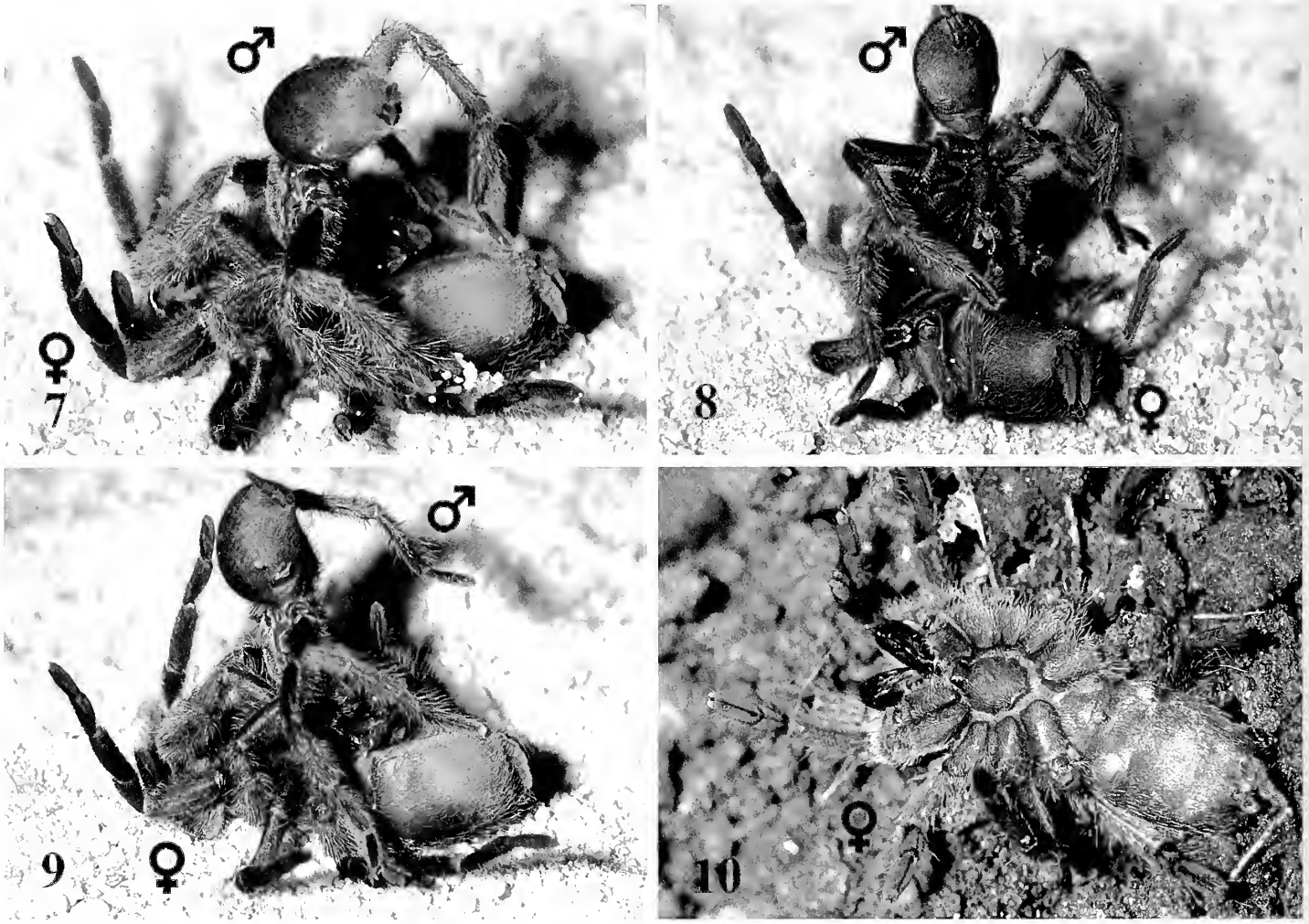
When bitten, the female remained motionless and the male sometimes continued mating or even calmly went away from



Figures 1–6.—*Sickius longibulbi* mating. 1. Male approaching the female, touching her with his anterior legs. 2. Male leg I tibial apophysis clasping the female fangs. 3. Male holding the female tightly with his legs III around her prosoma ("hug"). 4. Male touching the female's posterior legs with his legs III. 5. Male suddenly pushing the female in a very fast movement. 6. Female positioned with her back on the substrate. Photos: R. Bertani.

the female when the mating was over. In one mating sequence (pair 4), the male bit a female that was lying on the ground, walked on her, and then went away (Fig. 10). For several minutes, the female stayed totally immobile. Afterwards, she recovered and walked away. This type of behavior has not been described for any other theraphosid and may indicate that the male venom can be used to calm the female.

As shown above, several points in the mating behavior of *Sickius longibulbi* were clearly different from the prevalent theraphosid pattern. Theraphosid courtship usually consists of palpal and leg movements, body vibrations, and clasping (Yañez et al. 1999; Costa & Pérez-Miles 2002). In all species studied to date, the male positions himself in front of the female when mating, with both bodies tilted up and with the male extending his palps under the female and inserting them into her genital opening (Foelix 1996). Even in *Encyocratella olivacea* Strand 1907 (Gallon 2005) (formerly *Xenodendrophila gabrielli* Gallon 2003), the only other theraphosid known to lack spermathecae (Gallon 2003), courtship is similar to that of other tarantula spiders, with palpal tapping and body



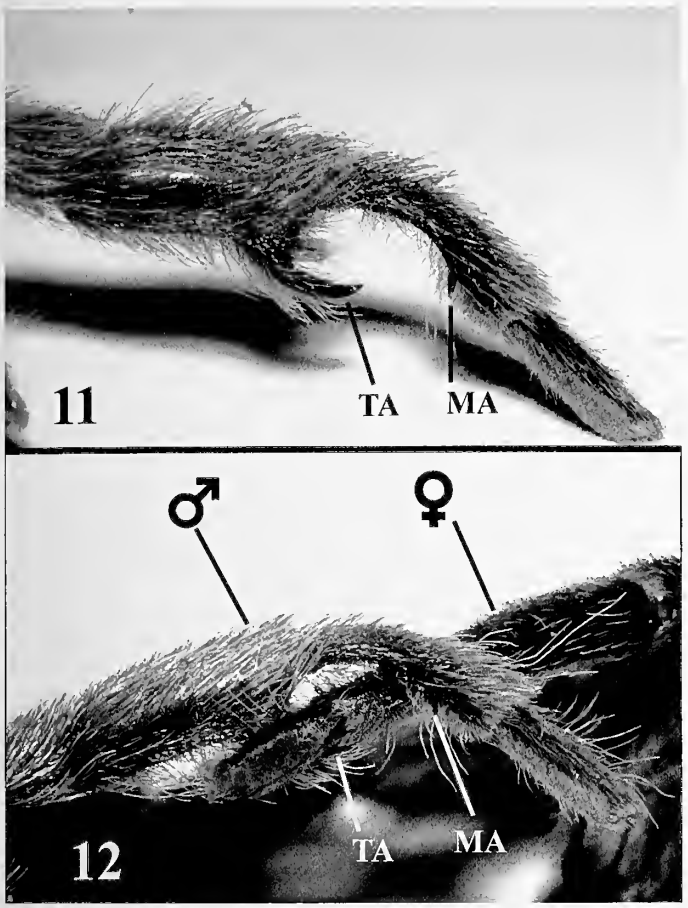
Figures 7–10.—*Sickius longibulbi* mating (continued). 7. Male trying to raise his body. 8. Male balancing himself in the air at an angle of 90° relative to the female body axis. 9. Insertions of male's long slender embolus into the female genital opening. 10. Female lying motionless on the ground after male bites her (pair 4). Photos: R. Bertani.

vibrations (Kumar 2004). Apparently, reproductive behavior of this species was not altered dramatically from the prevalent pattern by absence of the spermathecae.

In *Sickius longibulbi* the male only scratched his palps on the soil and performed inward movements of his leg III. We did not detect the complex movements like those observed by Costa & Pérez-Miles (2002) in *Acanthoscurria suina* and in other Uruguayan theraphosids. The typical pattern for female theraphosids is to tap their front legs in answer to male courtship, but we did not detect this for *Sickius longibulbi* except in one case in which the female was put in a cage with sand and soil many days before the mating attempt (pair 9 in Table 1). This female built a retreat on the soil and when the males approached and touched the retreat door, she answered by making faint tapping movement with her anterior legs. This suggests that in our other observations we did not see females answer male courtship because these females were put in the arena simultaneously and close together with the male.

Another difference when compared to other species was the behavior of the male *S. longibulbi* when approaching the female: he used his leg I tibial apophyses together with the leg I metatarsal apophyses to clasp the female's legs and to bring her close to him. After the male approached the female, he held the female's prosoma tightly with his legs I and II ("hug"). This behavior has not been reported before for any other theraphosid species. Normally, males of other species have legs I clasped, the legs II slightly touching the female and legs III and IV on the substratum (pers. obs). A high level of aggressiveness was evident in the mating behavior of *S. longibulbi*. The male usually bit the female, especially when he was holding her. This aggressive behavior is not commonly reported for mygalomorph spiders (Jackson & Pollard 1990; Shillington & Verrel 1997).

Something else unusual about *S. longibulbi* was that the male seemed to try to knock the female down: he pushed her entire body until she was lying on her back. This is quite different from the loss of equilibrium that has been reported in some Uruguayan species (Costa & Pérez-Miles 2002), as in those species it seems to be related to the spider's adaptation to mating in the entrance to burrows. In *S. longibulbi*, all the males tried to make the female fall over backward so that he could position himself angled up by 90° from the reclining female. The male's behavior in achieving this seems to demand a lot of energy. One of the possibilities of this unusual posture of the male is to make the male more successful at transferring sperm (i.e., in this posture, his extremely long embolus, longer



Figures 11–12.—*Sickius longibulbi* clasping apparatus. 11. Male, leg I. 12. Simulation of a male clasping female leg I. Photos taken from preserved specimens. TA = Male leg I tibial apophysis, MA = Male leg I metatarsal apophysis. Photos: R. Bertani.

than the palpal tibia length (see figs. 1–3 of Bertani & Silva Junior 2002), can deposit more sperm in the female's oviduct, which is where she retains the sperm because she does not have spermathecae). We cannot be certain that the behavior we observed is fully representative of what happens in nature because we did not observe any mating under natural conditions. However, one mating occurred in conditions that were probably quite similar to conditions in nature, with the female having constructed a retreat. In this instance, the male's behavior was comparable to male behavior under more artificial conditions. It has been noted before that spider mating in captivity does not appear usually to be especially distorted when compared to mating behavior in nature (Jackson 1988; Jackson and Pollard 1990), and it seems likely that our observations are, in basic respects, typical of *S. longibulbi*.

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Kin discrimination in the amblypygid, *Damon diadema*

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Abstract. Soeiality occurs in less than one percent of all arachnids. Prolonged subsocial behavior with amicable mother-offspring-sibling associations that extend for a ycar has recently been reported in captive amblypygids, *Damon diadema* Simon 1876 (whip spiders; order Amblypygi, family Phrynichidae; Rayor & Taylor 2006). Many social animals have the ability to discriminate kin from other conspccifics so that benefits of group-living are preferentially direeted toward kin, although kin diserimination is rare in soeial spiders. To aid in quantifying rates of behavior, we developed a behavioral ethogram of soeial and agonistic interactions in immature *D. diadema*. We conducted two experiments that demonstrate the ability of immature *D. diadema* to recognize and behave differentially toward kin. In a series of cross-introduction experiments, immaturc kin or non-kin were introduced into soeial groups to determine whether aggression and non-aggressive interaction rates varied based on their relationship to the resident animals. To tcst the hypothesis that differenees in behavior were due to familiarity with the habitat, rather than with kinship with resident animals, individuals were cross-introduecd into unfamiliar habitats with kin or non-kin. In these introduction expcriments, kinship determined the level of aggression among individuals while habitat familiarity did not have an effect. Using olfactory cues alone in Y-mazc choice experiments, 9-month old amblypygids discriminated their mother from an unrelated adult female and spent significantly more time near their mother. We discuss our results in relation to other examples of kin discrimination in insects and arachnids, and potential benefits to amblypygids at different ages.

Keywords: Whip spider, social behavior, kin discrimination, olfaction, ethogram

Although nestmate discrimination is well known among the social insects (e.g., Hölldobler & Wilson 1990; Vander Meer et al. 1998), it appears to be rare or absent in most of the subsocial and social arachnids (Lubin & Bilde 2007). Most social spiders readily accept unrelated individuals into colonies with no behavioral conflicts between kin and non-kin members of the colonies (D'Andrea 1987; Pasquet et al. 1997; Lubin & Bilde 2007). In most cooperative social spider species, immigration into the colonies is so rare and the costs of accepting non-kin into the group so minor, it has been hypothesized that the spiders have not evolved mechanisms for kin discrimination (Avilés 1997; Evans 1999). However, recent studies indicate that, although kin discrimination behavior is not expressed under normal circumstances in most social arachnids, at least some arachnids can differentiate between kin and non-kin. The social Australian huntsman spider, *Delena cancerides* Walckenaer 1837 (Sparassidae) that live in retreats under tree bark that are limited in size and availability selectively attack unfamiliar, non-kin that enter their colonies (Rowell & Avilés 1996; Yip & Rayor pers. obs.). In the social crab spider, *Diaea ergandros* Evans 1995 (Thomisidae), juveniles preferentially cannibalize non-kin in times of food scarcity, while subadult females cannibalize unrelated females and sibling males before immigrant males (a pattern that maximizes outbreeding opportunities) (Evans 1999). Similar preferential cannibalism of non-kin occurs in starved subsocial *Stegodyphus lineatus* Pocock 1898 (Eresidae) and social *Delena cancerides* (Sparassidae) spiders (Bilde & Lubin 2001; Beavis et al. 2007). Among the solitary spiders, there is some evidence that prior to dispersal in the third instar, individuals discriminate among siblings or familiar individuals to reduce cannibalism within the brood (Anthony 2003). Among the non-spider arachnids, kin recognition has only been seen in the highly social pseudoscorpion, *Paratemnoides nidificator* Balzan 1888 (E. Tizo-Pedroso pers. comm.).

Given the emerging evidence for some level of kin discrimination abilities in spiders, we chose to investigate the issue of kin discrimination in the prolonged subsocial amblypygid, *Damon diadema* (Simon 1876) (Order Amblypygi). Amblypygids have generally been characterized as solitary and intolerant of conspecifics (Weygoldt 2000). However, recent work on captive *D. diadema* suggests that this species may live in prolonged subsocial groups (Rayor & Taylor 2006). In captivity, immature *D. diadema* remain closely associated and highly interactive with their mother and siblings for approximately one year until becoming sexually dimorphic at 11–15 months of age (Rayor & Taylor 2006). Prolonged associations within the social groups include active aggregation, high levels of tolerance, and frequent amicable tactile interactions with their antenniform first legs ("whips") to neighboring individuals. Prior to sexual maturity, agonistic behavior within sibling groups or with the mother is rare and there is a strong tendency for immature siblings of all ages to closely associate with one another. *Damon diadema* are often found in cave habitats, where there may be multiple overlapping groups within a single cave (Weygoldt 2000). In such a habitat, we predict that if there are advantages to maintaining long-term associations with kin it would be beneficial for individual *D. diadema* to be able to determine whether another amblypygid was kin or non-kin. As recent evidence suggests that diverse organisms such as social insects and ground-dwelling squirrels use cues of familiarity to direct behavior appropriately (Dahbi & Lenoir 1998; Mateo 2004), we did not distinguish between familiarity and kinship in this study. As preferences for aggregating with kin have been consistently demonstrated in other social species (Krause &

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Table 1.—A list of the ages of members of eaeh clutch during each observation or experiment. *Birth indicates the day when the amblypygids descended from their mother's abdomen and were freely mobile. The mother of clutches 1 and 2 died of natural causes prior to all but the baseline observations of behavior. The mother of clutch 3 remained with her offspring for the duration of the study.

				Age during experiments		
Clutch	Date of birth*	Number in clutch	Mother's status	Baseline observations	Introduction experiments	Olfactory recognition experiments
1	15 Apr 2002	13	Died April 2003	10–11 mo	15–17 mo	–
2	25 Dec 2002	8	Died April 2003	–	7–9 mo	–
3	8 Jan 2003	20	Alive	–	7–9 mo	9 mo

Ruxton 2002), we predicted that *D. diadema* would be able to discriminate between kin and non-kin, displaying higher levels of aggression towards non-kin and interacting more with kin animals.

To investigate kin discrimination in immature amblypygids, we conducted a series of cross-introduction experiments. We introduced familiar kin or unfamiliar non-kin individuals into social groups to determine whether aggressive and non-aggressive interaction rates varied based on their relationship to the resident animals. To test the hypothesis that differences in behavior were due to familiarity with the habitat, rather than kinship with resident animals, we also cross-introduced individuals into unfamiliar habitats with kin or non-kin. We developed a behavioral ethogram to aid in quantifying the social and agonistie interactions observed in immature amblypgyids. Our second experiment tested the hypothesis that a young amblypygid is capable of distinguishing its mother from an unrelated adult female using only olfactory cues.

METHODS

Subjects.—*Damon diadema* (Order Amblypygi, Family Phrynichidae) are native to Tanzania and Kenya where they are found in caves or on buttressed trees in coastal forests (Weygoldt 1999). Adult females used in this study were wild-caught in the Usumbara Mountains of Tanzania and obtained through several dealers over a two-year period. Females were bred in the laboratory with wild-caught or first generation captive males. Due to time differences when the adult females were obtained, their source, and relative size (= age), we have no reason to believe that any of the adult females were related and know that none of the clutches shared fathers. Three clutches were used in this study; all were born and raised in captivity. Clutch refers to a cohort of same age siblings. Members of Clutches 1 and 2 were half-siblings by the same mother that were kept together for the duration of this study. The age of members of each clutch, the status of their mother, along with their ages during each experiment are given in Table 1.

To permit identification of individuals, young were individually marked on their carapace with Testor's enamel paint. Voucher specimens were deposited in the Cornell University Insect Collection and at the Smithsonian Institution National Museum of Natural History. Extensive video documentation of social interactions and behavioral responses during introductions are available through the Cornell University Laboratory of Ornithology, Macaulay Library. Video vouchers are archived in the Macaulay Library and can be found online at: http://animalbehaviorarchive.org. These videos can be located through an Advanced Search of the Notes for "Rayor Amblypygid Sociality" or by species name, Rayor, and behavior.

Housing and Diet.—Amblypygids from Clutches 1 and 2, and from Clutch 3 were housed in glass aquaria measuring 50 cm × 26 cm × 42 cm. To simulate natural habitat conditions and accommodate the amblypygids' thigmotactic preferences, cork bark lined the walls of the aquaria. A soil/vermiculite substrate on the floor helped maintain humidity. Water was supplied in a water dish and misted onto the bark. Animals were fed live domestie crickets (*Acheta domesticus*) approximately twice weekly. They were maintained at room temperature (~ 25° C) and largely kept in the dark. Behavioral observations were made in the dark under red light using a Sony digital camcorder (model DV-TRV30 NTSC), with "nightshot" infrared lighting.

Behavioral repertoire.—Although behaviors involved in courtship and fighting have been described for some species of amblypygids (Weygoldt & Hoffmann 1995; Weygoldt 2000; Fowler-Finn & Hebets 2006), no comprehensive behavioral repertoire or ethogram has been published that describes the characteristic behaviors involved in social interactions among immature amblypgyids and their mothers. An ethogram of key behaviors pertinent to social interactions was developed for *D. diadema* to quantify rates of behavioral interactions (Table 2). Behaviors associated with adult conflict or courtship were omitted. Descriptions of *D. diadema* behaviors were based on four years of observations from test subjects in this study and the larger number of individuals of all ages reported in Rayor & Taylor (2006).

Introduction experiments.—To assess rates of aggressive and non-aggressive interactions in an undisturbed situation, baseline observations of 12 immature individuals from Clutch 1 were observed for a total of 12 h. To evaluate the differences in behavioral responses of young amblypygids to familiar kin (K) and unfamiliar non-kin (N), and to familiar (FH) and unfamiliar habitats (UH), we introduced single focal individuals into social groups in each possible combination in 27 one-hour "introduction experiments" (Table 3). All kin were siblings (or half-sibs) that were familiar to one another, while all non-kin were unfamiliar with each other; we did not separate the effects of familiarity from kin discrimination based on other cues. In each introduction trial, one animal was removed from its natal group, left in isolation for a minimum of one hour and reintroduced into either its natal group or to an unrelated group. To distinguish between differences in the introduced individual's response to unfamiliar conspecifics compared to responses due to an unfamiliar "habitat" (cage), we also varied the locations where introductions took place. In

Table 2.—Behavioral repertoire involved in social and foraging interactions of immature *D. diadema*. Behaviors are divided into two categories: (a) those involving the whip and (b) those involving other parts of the body.

(b) Body postures, movements, and behaviors

Behavior Name	Category	Description
Slow scan	N/A	Specific details of movement may vary, but whip movements are slow and context indicates that the animal is relaxed and carrying out routine scans of the area nearby.
Inspect	Interaction	Angle subtended by whip motion is small; whip movement is focused in a specific area, but whip does not necessarily contact another object or animal.
Touch whip	Interaction	The focal individual makes contact with another amblypygids's whip.
Touch other amblypygid	Interaction	An individual touches its whip(s) to any part of another amblypygid's body, excluding the whips or palps.
Touch palps of other	Interaction	The focal individual touches its whip(s) to any part of the palps of another amblypygid or to the nearby region (chelicera).
Touch by other	Interaction	Focal individual is touched by the whip of another amblypygid.
Touch non-amblypygid	Interaction	An individual makes whip contact with a non-amblypygid object (e.g., a prey item).
Flinch whip	Interaction, Aggression	The whip is briefly and quickly jerked, usually backward. Most commonly seen after animal contacts another amblypygid or prey item.

(b) Body postures, movements, and behaviors

Behavior Name	Category	Description
Relaxed closed	N/A	Amblypygid's body is flat against the substrate, and palps are closed. Typical resting posture.
Relaxed open	N/A	Amblypygid's body is flat against the substrate, but palps are open. Contrasts with palp opening during aggression in that palps loosely drop open, often with the femur at ~ 45° hanging downwards. Occurs in relaxed contexts, as a typical resting posture.
Agonism low	Aggression	Palps are opened such that the angle between the femur and tibia is less than 90°. Right and left palps are usually in symmetrical positions. Palps typically open rapidly and are briefly held open before returning to the "relaxed closed" posture.
Agonism high	Aggression	Similar to Agonism low, but femoral/tibial angle is greater than 90° and typically held open for a significantly longer period. Indicative of a higher level of aggression.
Bat/swat palps	Aggression	One or both palps are opened and swung through the area in front of an amblypygid. The speed of this movement is generally not as fast as that seen when an individual is making a grab at another amblypygid or prey item. Possible context: locating another animal prior to making a grab at it.
Grab	Aggression	Both palps are moved simultaneously towards another animal. This movement is quick and clearly aggressive (possibly an attempt to remove the other animal's whip or leg). Movements are essentially the same as during prey capture, but context is interaction with another amblypygid.
Body elevated off substrate	N/A	Legs are straightened more than during typical resting posture, such that the amblypygid's body is no longer in contact with the substrate. May indicate heightened alertness; often seen in contexts of aggression or hunting.
Body pump	Aggression	Body is moved up and down as amblypygid bends and straightens its legs. Contexts are aggression and hunting.
Walk	N/A	Amblypygid walks across substrate, usually conducting whip scans as it moves.
Retreat	Aggression	Focal individual moves backwards, usually away from another amblypygid or prey item.
Erratic Run	Aggression	The animal moves across the bark at a speed faster than normal walking, periodically stopping and starting. Usually accompanied by quick movements of the whips in broad arcs. Animal often appears to be agitated, making efforts to quickly investigate its new surroundings.
Fast run	N/A	Usually seen in response to touching the base of an amblypygid's legs. The animal moves across or to the other side of the bark extremely quickly, apparently without stopping during the run to make whip inspections of its surroundings.
Orient to prey/prepare to attack prey	N/A	Palps are drawn back to open position—femoral/tibial angle usually is not more than 90°, but angle between palp and body is small. Both whips are usually in the area near the prey item, repeatedly and briefly touching the prey. The amblypygid's body is oriented facing the prey. This behavior is usually followed by grabbing at the prey.
Grab at prey	N/A	Both palps move synchronously from open position towards prey.

Table 2.—Continued.

(b) Body postures, movements, and behaviors

Behavior Name	Category	Description
Capture prey	N/A	Prey is impaled on the metatarsal spikes, at the end of the palpal hands. If the first capture attempt is unsuccessful, an individual may make several additional grabs at the prey item.
Drop prey	N/A	Prey is released from palpal hands. May occur while prey is still alive, or after it has been killed; may be accidental or intentional.
Eat prey	N/A	Amblypygid holds prey in palpal hands during consumption, may move hands, and adjust position of prey. Chelicerae move up and down, masticating prey.
Groom	N/A	Includes several behaviors such as back and forth movements of the palps, drawing of the whips through the chelicerae, or chewing on the tip of the whips or legs with the chelicerae.

K-FH trials, the test subject was returned to its natal cage with its siblings who had remained undisturbed. In K-UH trials, the test subject's entire sibling cohort was moved to a novel cage with unfamiliar bark, allowed to adjust to the cage overnight and then the test subject reintroduced. In N-FH trials, the test subject's kin were removed from their natal cage temporarily, the unrelated cohort was introduced into the test subject's natal cage, allowed to adjust overnight, and the unrelated test subject introduced. In N-UH trials, the test subject was introduced to a cage of unfamiliar individuals who had not been disturbed otherwise. In each introduction trial, the introduced individual was observed for one hour immediately following transfer.

Observations were videotaped under red light, behaviors were recorded on a handheld Psion Workabout (a PDA), and later analyzed using Noldus Observer 4.0 behavioral software. Introduced individuals were observed using focal sampling and all reported behavior reflects those of the introduced individual. Behaviors were attributed to initiated behaviors (I) or received behaviors (R), although the focal sampling method does not clearly reflect the extent that most behaviors involving whip contacts were often reciprocal. We assessed interaction rates, using the following non-aggressive interactive behaviors between individuals: whip-whip touches (I or R), touching another individual's body or legs (I), touching the palps of another individual (I), getting touched by another amblypygid (R), whip flinches (R) (Table 2). To assess aggressive events, we included all behaviors that were consistently observed in aggressive contexts: body pumping (I), agonistic palp opening (both low and high levels of agonism – I), grabbing or swatting with palps (I), retreating (R), and erratic running (R). The aggressive behaviors ranged from retreating to clear threats (body pumping or agonistic palp opening, erratic running away), to active aggression (grabbing or swatting with palps). Swatting or grabbing with palps is as serious as aggressive behaviors get among immature *D. diadema*. We have no direct or indirect evidence of immature individuals engaging in serious conflicts or cannibalism in this study or previous studies (Rayor & Taylor 2006). During observations for baseline and introduction experiments, the adult females were largely uninvolved in behavioral interactions with their offspring, so that they were excluded from these analyses.

Table 3.—Design of the Introduction experiments, number of focal individuals observed and the code for each experiment. Kin were all familiar siblings or half-sibs, while Non-kin were unfamiliar and unrelated individuals. Each trial lasted 1 h.

	Animals	
Habitat	Kin	Non-kin
Familiar	K-FH $n = 7$	N-FH $n = 7$
Unfamiliar	K-UH $n = 7$	N-UH $n = 6$

For each introduction experiment we calculated the number of total, initiated, and received non-aggressive interactions and aggressive behavior by the introduced focal animal. There were so few received aggressive behaviors that only total aggression was statistically analyzed. Rates were calculated as the number of aggressive interactions per hour. To examine the effect of different sets of predictors on the response variables of aggressive or non-aggressive interaction rate four sets of 2-way ANOVA's were carried out. The best models included both kinship with the resident social group and familiarity with the habitat as predictors. For total, initiated, and received aggression and interaction rates, we tested for effects of kinship (kin (K) vs. non-kin (N)), habitat (familiar (FH) vs. unfamiliar (UH)), as well as the interaction between kinship and habitat. All aggression data were log transformed to achieve normality, while interaction data were normally distributed without transformation. To avoid complications associated with pseudoreplication, we minimized the number of times each individual was used in each series of experiments. The kin introduction experiments were designed such that the potential for animals from different cages to become familiar with each other was limited. Although young were involved as residents in multiple kin introduction trials, only two individuals from Clutch 2 were used as the introduced animal in more than a single trial (but not in the same experimental context).

Olfactory Recognition Experiments.—To determine whether olfactory cues play a role in discriminating familiar from unfamiliar females, we evaluated the behavioral response of immature amblypygids to olfactory cues from their mother and an unrelated adult female in an "olfactometer." The vertically oriented Y-shaped olfactometer was composed of three 7.5 cm diameter clear acrylic tube arms connected through a "choice chamber" or a black 3-way plumbers joint

with a clear plexiglass window (Fig. 1). The arms included the introduction arm (61 cm long) through which the test subject was introduced, and two 48 cm long choice arms. The introduction arm had a removable window through which the test amblypygid was introduced. The plastic floor of the tubes was overlaid with mesh screening to provide a gripping surface for the amblypygid to walk on. At the end of each choice arm, the test amblypygid's mother and an unrelated, unfamiliar adult female were in 8 cm long screened containers. A double layer of wire mesh screen separated the choice arm from the females' containers, allowing airflow over the females but preventing any physical contact (including whip contact) between the test subject and the females. Air was pulled through the olfactometer by a slow fan affixed to the end of the introduction tube, resulting in air flowing from the females' containers upwards through the choice chamber, and past the point of introduction. Within the introduction tube and choice chamber, the test subject was potentially exposed to chemosensory cues from both adult females, but likely only exposed to cues from a single female within each choice arm. The position of the mother and unfamiliar female were randomized between trials. All trials were conducted in the dark under red light. Between trials, the apparatus was cleaned with ethanol.

The test subject was able to wander freely within the olfactometer. During each trial, the duration of time that the amblypygid spent in each region (0–6) within the olfactometer was recorded. Region 4 was always used to designate the side of the apparatus containing the mother, regardless of whether the mother was on the left or the right side of the apparatus. Additionally, the number of times that an individual passed between regions was recorded. Thus, the olfactometer evaluated whether immature amblypygids oriented toward and spent more time near their familiar mother based on olfactory cues alone. Trials were conducted for 45 min. The experimental subjects included each of the 15 members of Clutch 3 when they were 9 months old. Test subjects were only used once. The mother of Clutch 3 and the same unfamiliar adult female were used in all trials. Wilcoxon signed rank tests were used to compare the time test subjects spent near the mother and near the unrelated female. Mean time spent in each region of the testing apparatus was compared using a Kruskal-Wallis test. General activity levels of test animals were measured by determining the number of times a test subject moved between regions during the trial.

RESULTS

Behavioral Observations.—The sensory and social lives of amblypygids are centered on the thin antenniform first pair of legs (or "whips"), which are extensively used for odor discrimination (Hebets & Chapman 2000), spatial location (Hebets 2002), and tactile contact between individuals (Rayor & Taylor 2006; Rayor 2007). The whips are covered with sensitive chemosensory and mechanosensory setae (Foelix et al. 1975; Foelix & Hebets 2001; Spence & Hebets 2006), and are capable of delicate movements approximately 340° around the horizontal axis of their bodies, as well as vertical movement above the body (pers. obs.). Both amicable and agonistic social interactions were mediated primarily through whip movements or whip contact between individuals,

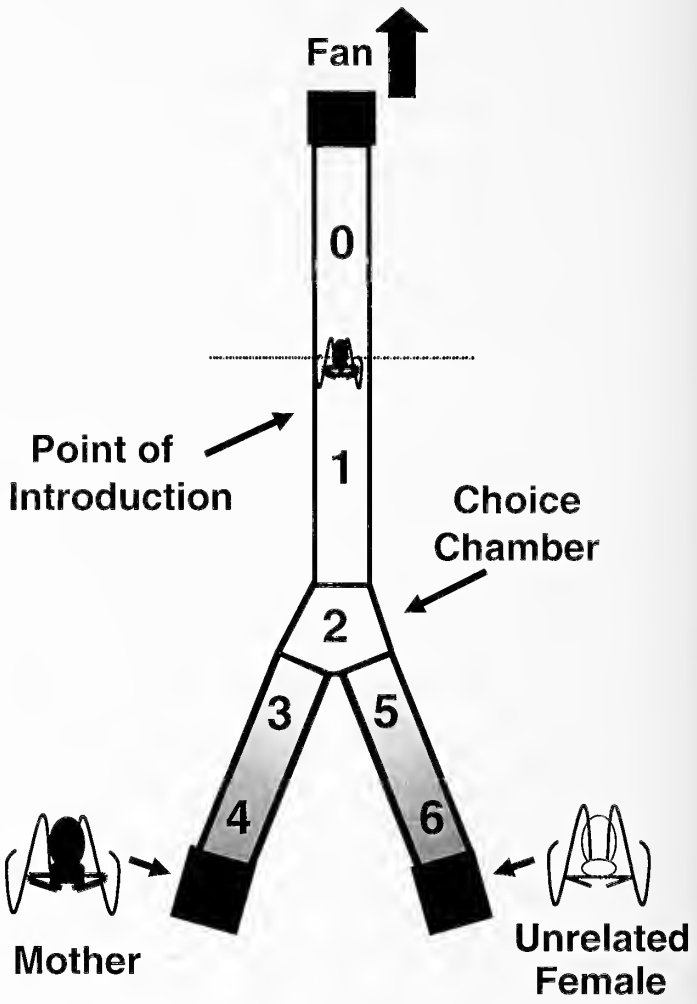

Figure 1.—Diagram of olfactometer with each of the numbered regions where the test amblypygid could move within the olfactometer. The fan pulled air from the adult females through the olfactometer. The choice chamber (Region 2) joined the three arms of the olfactometer and received odors from both females. The mother and unrelated female were separated from the main body of the olfactometer by a double layer of mesh screen.

although agonistic palp movements also played a role (Table 1). Particularly in social or novel situations, amblypygids' whips are in continuous motion exploring the environment and their neighbors. Animals frequently touch each other with their whips, speeding up whip motions when highly excited or agitated. Whips are moved in broad sweeps or in short localized taps. Palps are opened in the context of prey capture and aggression, and occasionally when an individual is relaxed and at rest. Specific positions of the palps and contextual information are almost always sufficient to determine whether an amblypygid is opening its palps in the context of aggression, predation, or relaxation (Table 2). Compared to overt whip and palp movements, changes in body posture were less apparent with the exception of dorsoventral pumping of the body and/or stilting of the legs, which indicated heightened aggression.

Introduction Experiments.—Baseline observations of undisturbed 11–12 month old siblings from Clutch 1 show a relatively low rate of aggressive and non-aggressive interactions (Fig. 2, 3). As all introduction experiments involved

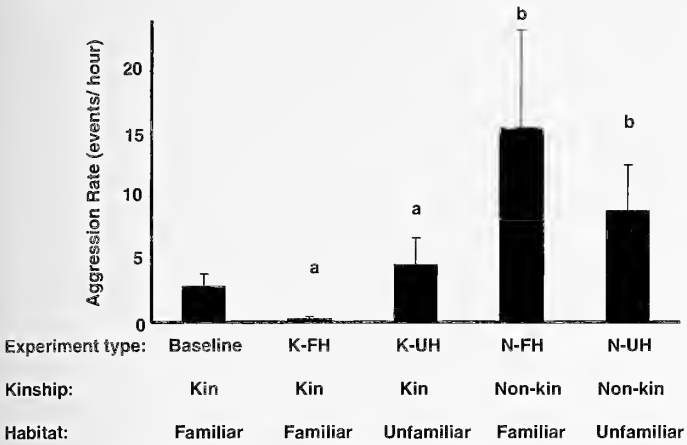

Figure 2.—Rates of aggression in each of the five treatments. Standard Error bars for total aggression are shown.

members of Clutches 2 and 3 when they were younger (7–9 months old), we only compared baseline observations with those of K-FH, which differed in the level of disturbance associated with removing and reintroducing a member of the group but not in kinship or familiarity with the habitat. There were no significant differences in interaction rates between these two groups. Aggressive behaviors were significantly more common during baseline observations ($F_{1,18} = 8.98$, $P = 0.0081$, Adjusted $R_2 = 22.0$) than K-FH. Because aggression rates increase as *D. diadema* become sexually dimorphic at 11–14 months (Rayor & Taylor 2006), we anticipated more aggression in the baseline observations than were observed.

In introduction experiments, resident animals rapidly interacted with the introduced individual. Compared to the behavior of residents, the behavior of the focal introduced animal was often hesitant; its movements jerkier and more agitated. Although interaction rates of the introduced subjects were relatively high in all experiments (events per hour: median = 144, range = 7–324), rates of aggressive interactions were consistently low among K-FH (events per hour: median = 0, range = 0–1) compared to N-FH (events per hour: median = 4, range = 0–51). Even among the focal individuals in N-UH, which experienced the most social disruption, aggression was primarily expressed through low level behaviors (body pumping and low agonistic palp opening). The low level aggression of immature *D. diadema* is in sharp contrast to the significantly more aggressive behaviors characteristically observed when unfamiliar adults are introduced to one another (repeated swipe palp, grappling, fencing position; Weygoldt 2000; pers. obs.) that may cause serious injuries or result in cannibalism.

Young amblypygids recognize non-kin and behave differentially toward them based on introduction experiments (Fig 2). The best aggression rate model included animals and habitat as predictors (2-Way ANOVA: Aggression: $F_{2,\ 26} = 4.045$, $P = 0.0306$, adjusted $R_2 = 19.0\%$). Kinship determined the rate of aggression involving the introduced individual (Kinship: $F_{1,\ 26} = 6.96$, $P = 0.0144$), but familiarity with the habitat had no impact ($F_{1,\ 26} = 1.3$, $P = 0.25$). Aggression rates were significantly higher for non-kin than kin (Least Square Means ± SE: Kin = 0.702 ± 0.307; Non-kin = 1.85 ± 0.32).

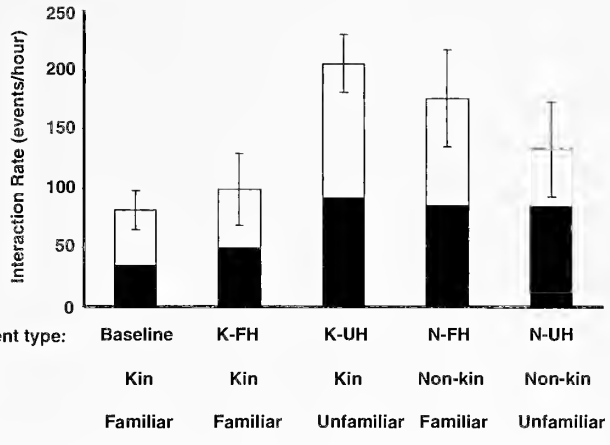

Figure 3.—Rates of non-aggressive interactions in each of the five treatments divided into initiated behaviors (black) and received behaviors (white). Standard Error bars for total interactions are shown.

No aspect of non-aggressive interactions (total, initiated, or received) differed significantly among introduction experiment treatment groups in 2-Way ANOVA comparisons (Fig 3). Interaction rates were relatively high with 1.65 to 3.4 events per minute, primarily due to whip-whip touches, but did not significantly vary between treatment groups.

Olfactory Recognition Experiments.—Immature amblypygids were able to differentiate between their mother and the unrelated female using only olfactory cues. Most of the experimental individuals were active, extensively exploring the olfactometer. Twelve of the fifteen immature amblypygids left the introduction tube and choice chamber to explore one or more of the choice arms that had their mother or an unrelated female at either end. Over the entire 45-minute trial young from Clutch 3 spent significantly more time in the distal segment of the choice arm (Region 4) closest to their mother than in the area (Region 6) closest to the unrelated female (Wilcoxon signed rank test: $T+ = 62$, $n = 12$, $P < 0.0386$). However, there was no difference between the total time spent in the mother's entire arm (Regions 3 and 4) compared to the unrelated female's arm (Regions 5 and 6) (Wilcoxon signed rank test: $T+ = 49$, $n = 12$, $P = 0.2349$). In the initial movement into the choice arms equal numbers moved toward the mother and the unrelated female ($n = 6$ each). Three young explored only the mother's side of the olfactometer; nine explored both the mother's and unrelated female's sides. None of the experimental subjects explored only the unrelated female's side of the olfactometer. The majority of the focal individuals actively explored the olfactometer; the mean number of region changes over the duration of the trial was 14.93 ± 7.69. There were no differences in the mean number of region changes based on whether an animal moved to the mother or unrelated female's region first (Mann-Whitney U-test: $U = 18.5$, $n_{mom} = 6$, $n_{unrelated\ female} = 6$, $P = 0.937$) or spent more total time near the mother (Region 4) or the unrelated female (Region 6) (Mann-Whitney U-test: $U = 20.5$, $n_{mom} = 8$, $n_{unrelated\ female} = 4$, $P = 0.461$). Together these results suggest that olfactory cues are sufficient for kin discrimination and that once the young had located their mother the familiar stimulus was sufficient to arrest their movements.

DISCUSSION

Our results suggest that immature *Damon diadema* respond differentially to kin and non-kin in the contexts of encountering unfamiliar individuals and in being more attracted to the olfactory cues from their mother. In all introduction experiments, the introduced nonkin individuals were significantly more aggressive than introduced kin. Although all individuals in a group were disrupted when moved to an unfamiliar habitat, familiarity with the habitat did not consistently affect the introduced individual's level of aggression compared to kinship. Our low sample sizes in this experiment could have resulted in an underestimate of the effects on behavior of manipulating the habitat. However, in the field, immature amblypygids almost certainly encounter unfamiliar individuals of all ages and potential threat, while most clutches are unlikely to be moved communally into unfamiliar habitats.

In olfactory recognition experiments, immature *D. diadema* were capable of discriminating their mother from unfamiliar adult females using only olfaetory cues. As these results are based on the behavior of only a single clutch, further research will be required to document the full role of olfaction in kin discrimination in amblypygids. Hebets & Chapman (2000) have demonstrated that amblypygids are much more attuned to chemosensory cues than the other arachnids. In the field, adult male amblypygids (*Phyrnus parvulus* Pocock 1902) use olfactory cues to locate reproductively mature adult females Hebets (2002). So it is not unexpected that these cues may be used in a social context in amblypygids. Use of olfactory cues for kin recognition is widespread in eusocial insects (Vander Meer et al. 1998), but has not been demonstrated in social spiders probably due to minimal costs associated with a lack of kin recognition in most of these social groups (Lubin & Bilde 2007). Amblypygids actively moving around while foraging at night are more likely to come in contact with unrelated animals than web-based social spiders foraging within the confines of their web. Among the spiders, olfaction has been demonstrated primarily in the sexual attraction of male to female spiders using short-range volatile cues on silk (Schulz 2004; Gaskett 2007).

Kin recognition abilities have been proposed to be advantageous in permitting nepotism among group members and for inbreeding avoidance (Sherman et al. 1997). Spatial overlap among individuals from several *D. diadema* clutches may occur within certain habitats, such as caves. The conundrum is to determine the context in which kin recognition is valuable to young amblypygids living in prolonged subsocial groups. Unlike the obvious advantages of group-living in the other arachnids (e.g., cooperative capture and sharing of prey, communal construction of retreat or web), Rayor & Taylor (2006) found few benefits of sociality in *D. diadema* beyond maternal defense of immature offspring. In the laboratory, sibling competition over prey is minimal (Rayor & Taylor 2006), although competition may be more intense in the wild. While there may be microclimate or warning advantages when young siblings pack together into small crevices during the day as they do in the laboratory, it is improbable that suitable crevices are so limited that there is the need to exclude non-kin from these sites in the wild. Nor does the need for kin recognition appear to be generated by aggressive behavior of the adult females: In the laboratory, two mothers with clutches readily accepted non-kin young (close in age to their own offspring) who were introduced into their cages, and the mothers were amicable to their own subadult offspring after a separation of two months (unpublished data).

The most parsimonious explanation for kin recognition in *D. diadema* is that while immature animals are capable of kin recognition, the ability to recognize kin pays dividends once they disperse from the natal social group and encounter, or become, aggressive adults themselves. The only amblypygid which has been observed extensively in the field is *Phrynus parvulus* whose adults can be both territorial or wander widely within the habitat (Hebets 2002). For adult *D. diadema*, similar movements leading to encounters with other amblypygids are probable. The low level aggression of immature *D. diadema* is in sharp contrast to the aggressive fights observed when unfamiliar same-sexed adults encounter one another (Weygoldt 2000; Fowler-Finn & Hebets 2006). We hypothesize that the ability to recognize kin, using a variety of cues, may help reduce serious conflicts among familiar amblypygids later in life. We speculate that if adult amblypygids recognize their siblings as adults, this will result in fewer injuries within kin groups and aid in inbreeding avoidance. Further research on the role of kin discrimination and social behavior in amblypygids will broaden our understanding of a taxon better known for its solitary and aggressive behaviors.

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Behavioral mimicry in *Myrmarachne* species (Araneae, Salticidae) from North Queensland, Australia

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Abstract. Batesian ant mimics – such as salticids belonging to the genus *Myrmarachne* – resemble their models to deceive potential predators, sometimes including the ants themselves. *Myrmarachne* species in addition to being striking visual mimics of ants also wave their first pair of legs in the air, much like the antennal movement of ants. Whether this leg movement is part of *Myrmarachne* species' mimicry is debated. In this study the leg I movement of four *Myrmarachne* species was investigated, with particular attention given to the frequency and amplitude of the leg waving. Correlations between the leg waving and other behaviors of *Myrmarachne* species were also looked at. There were interspecific differences in leg I movements, and the leg I waving also depended on other behaviors such as "bobbing" the opisthosoma. Thus the leg I movement of *Myrmarachne* species is behavioral mimicry of the antennal movement of ants, in other words increasing the spiders' resemblance to the ants to avoid predation. This "antennal illusion" displays characteristics of a plastic trait which has evolved under selection pressure.

Keywords: Behavior, antennal illusion, mimic, myrmecomorphy

Ant-mimicry in arthropods, the morphological, chemical and/or behavioral resemblance of specialized arthropod species to ants (Rettenmeyer 1970; McIver & Stonedahl 1993), is widespread and has - specifically in spiders - evolved repeatedly in families such as the Salticidae and the Clubionidae (for review see Cushing 1997). Batesian (Bates 1862) ant mimics must live in sympatry with their models, resembling their noxious or aggressive model thereby deceiving potential predators and thus gaining protection. The selection pressure exerted by predators is strong and, as a consequence, traits associated with Batesian mimicry are expected to evolve rapidly (Mappes & Alatalo 1997). The resemblance of Batesian mimics of ants to their models (also known as myrmecomorphs) can be both morphological and behavioral. A constriction in the middle of the carapace and a shiny opisthosoma shaped similarly to the ant's abdomen are some of the morphological adaptations of ant-mimicking spiders. The constricted carapace gives the spider the appearance of a three-segmented body like that of ants, whereas the shiny look of the opisthosoma - obtained through the presence of specialized or scale-like setae – and its shape further increase the mimic's resemblance to the ant (McIver & Stonedahl 1993).

Myrmecomorphs often reinforce their morphological resemblance to ants through ant-like behaviors. These behaviors include walking in a zig-zag motion (Reiskind 1977; Pekár & Král 2002), moving their opisthosoma up and down ("twitch abdomen" in Jackson 1982) in a manner similar to gaster bobbing in ants, and waving their first pair of legs in the air while walking on the remaining three pairs (Reiskind 1977). This movement of the first pair of legs in myrmecomorphs is generally thought of as behavioral mimicry, and has therefore been termed "antennal illusion" (Reiskind 1977). In some cases however, this leg movement is carried out by spiders to detect chemical cues from ants, as in the ant-eating zodariid spider *Habronestes bradleyi* (Pickard-Cambridge 1869) (Allan et al. 1996). Thus, the purpose of this leg I movement is not always clear as Pekár & Král (2002) stipulate in their study on *Zodarion*, suggesting that the "antennal illusion" of these spiders could be a form of threat display towards the ants rather than a means of detecting airborne chemicals. The leg I movement can vary greatly among species as well as between males and females of the same species, as was found in a species of *Sarinda* cited by Jackson & Drummond (1974) as *Sarinda linda* Reiskind (not listed in Platnick 2008).

Myrmarachne McLeay 1835 (Araneae, Salticidae) is a highly speciose genus of salticids whose species bear a striking resemblance to different ant species with which they associate closely and whose individuals also wave their first pair of legs in the air (Mathew 1954; Edmunds 1978; Jackson 1986). Since many ant species are aggressive and attack animals not belonging to their colony (Hölldobler & Wilson 1990), the close association of ant-mimics with ants can be dangerous (Halaj et al. 1997; Nelson et al. 2004; Nelson et al. 2005). *Myrmarachne* species, however, have developed special behaviors allowing them to deal with the aggressive nature of ants (Ceccarelli 2007) and, as myrmecomorphs have been shown to have higher rates of survival than non-ant associating spiders (Edmunds 1993; Nelson et al. 2004), establishing that these spiders are Batesian mimics. *Myrmarachne* species are diurnal, and rely heavily on visual, rather than chemical cues (Nelson & Jackson 2007), which means that they are unlikely to wave their legs I as a means of picking up chemical cues.

Using four *Myrmarachne* species as examples of Batesian mimics, this study investigates the nature of leg I movement in these salticids. The questions addressed are how do leg I movements differ between *Myrmarachne* species and sex, how do other behaviors influence these movements, and is there a relationship between leg I movement of each *Myrmarachne* species and antennal movement of the corresponding ant species? These questions help us understand the nature of leg I movement in a typical Batesian ant-mimic. If the leg I movement is a means of picking up chemical cues we would expect it to be much more random than if it is really a Batesian mimicry trait. In contrast, if the leg I movement is a component of Batesian mimicry we would expect this behavior to display properties similar to other traits under selection pressure, such as interspecific differences and plasticity.

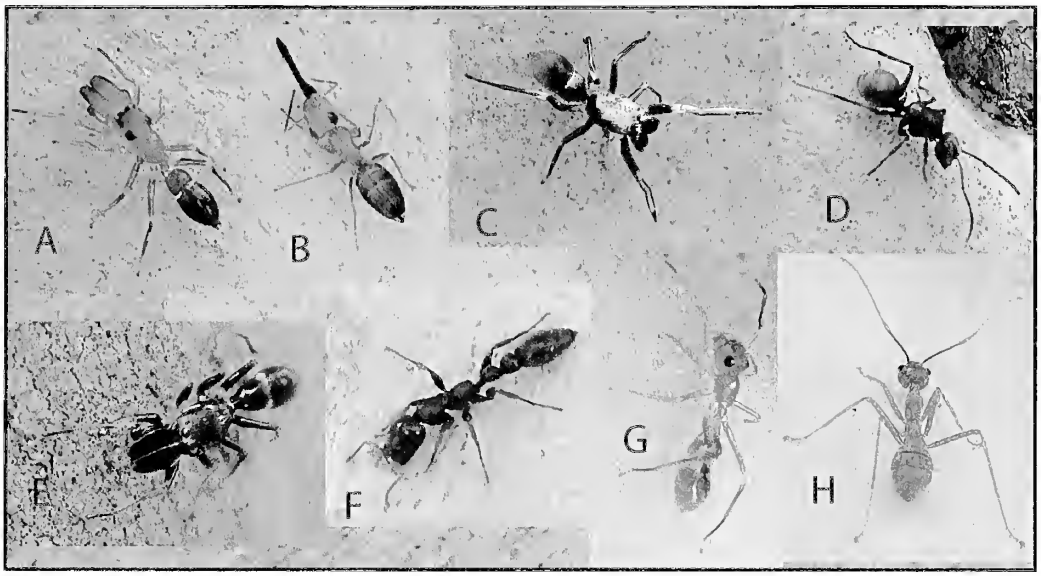

Figure 1.—Paired photographs of *Myrmarachne* mimics and their respective model ant speeies from Townsville. *Myrmarachne* sp. A (A) and model ant *Opisthopsis haddoni* (B); *Myrmarachne* sp. B (C) and model ant *Polyrhachis* nr.*obtusa* (D); *Myrmarachne* sp. D (E) and model ant *Tetraponera punctulata* (F); *Myrmarachne* sp. F (G) and model ant *Oecophylla smaragdina* (H) (modified from Ceccarelli & Crozier 2007).

METHODS

This study was carried out at the James Cook University campus in Townsville, North Queensland, Australia (19°13′S, 146°48′E) using sympatric species of local *Myrmarachne* (species used here designated sp. A, B, D, and F) and their respective model ant species. The *Myrmarachne* species are undescribed to date, but species integrity has been established through DNA analysis (Ceccarelli & Crozier 2007) and taxonomic work is under way. Mimic-model associations between *Myrmarachne* and sympatric ant species were determined visually by identifying the ant species that had the closest morphological resemblance to each *Myrmarachne* species (see Fig. 1). In addition, each *Myrmarachne* species was collected within a 5 meter radius of a determined model ant species' colony.

Voucher specimens of all species used in this study have been deposited in the arachnid and entomology collections of the Queensland Museum (Brisbane, Australia) with the following accession numbers: S66648 (*Myrmarachne* sp. A); S66649 (*Myrmarachne* sp. B); S66650 (*Myrmarachne* sp. D); S66651 (*Myrmarachne* sp. F); T133706–707 (*Opisthopsis haddoni* workers); T133693–696 (*Polyrhachis* nr. *obtusa* workers); T133697–699 (*Tetraponera punctulata* workers); T133700–702 (*Oecophylla smaragdina* workers). The numbers of individual females and males for *Myrmarachne* species used in this study are shown in Table 1. For the ants, 15 individuals from each species were used.

The animals were collected and brought into the lab for video recording. An individual *Myrmarachne* and one ant (random model or non-model) were videotaped inside a 10 cm diameter Petri dish. Recordings were made for 1 h, on each occasion using a different pair of animals as well as a new Petri dish, thus avoiding possible effects on behavior from chemical cues left from a previous encounter. The recording was carried out using a low light, high resolution video camera connected to a video recorder. The subsequent analysis was done using a SVHS player connected to a computer, using the program Adobe Premiere (version 4.2). The hour-long recordings were parsed twice, each time recording different variables from different parts of the tape.

During the first videotape pass, twenty instances were analyzed (the first ten at the start of the recording and the next ten starting from 30 min into the tape) when the spider showed a reaction to the presence of the ant. The analysis involved recording whether the spider was waving its first pair of legs, lifting them up without waving them, and/or bobbing its opisthosoma (as shown in Table 2). These data were recorded to find out how often *Myrmarachne* wave their legs I (as opposed to carrying out other forms of behavior) when encountering ants and provided us with count data on how frequently the spiders carried out each behavior.

The second videotape pass involved taking ten measurements per hour (every 6 min) of the frequency (cycles per second) at which *Myrmarachne* individuals waved their first pair of legs and the amplitude (in mm) of the leg movement.

Table 1.—Numbers of male and female *Myrmarachne* of each species used in this study

Myrmarachne species	A	B	D	F
Females	9	8	9	10
Males	6	7	6	5

Table 2.—Behavioral traits observed in *Myrmarachne* species

Behavior	Explanation
none	neither waving the legs nor bobbing the opisthosoma
wave	waving the first pair of legs up and down
bob	only bobbing the opisthosoma
wave + bob	waving the first pair of legs up and down and bobbing the opisthosoma at the same time
lift	first pair of legs raised in the air and held there without the up-and-down movement

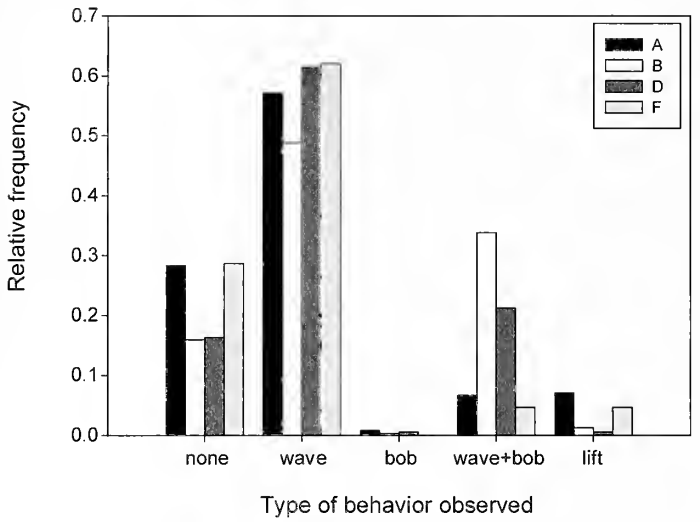

Figure 2.—Relative frequencies of the type of behaviors (as described in Table 2) of all four *Myrmarachne* species (A, B, D, and F). (χ^2_{12} = 142.69, $P < 0.001$).

When measuring the frequency, one cycle was taken to be the movement of the leg from one point through both top and bottom extremities and back to the starting point. The amplitude was measured from the highest apex of the tip of leg I to the substrate. To avoid negative values, the substrate was chosen as a starting point for the amplitude measurement since the leg I waving often started from the substrate. At the same time co-occurring activities were recorded, namely whether or not the *Myrmarachne* was moving (walking or

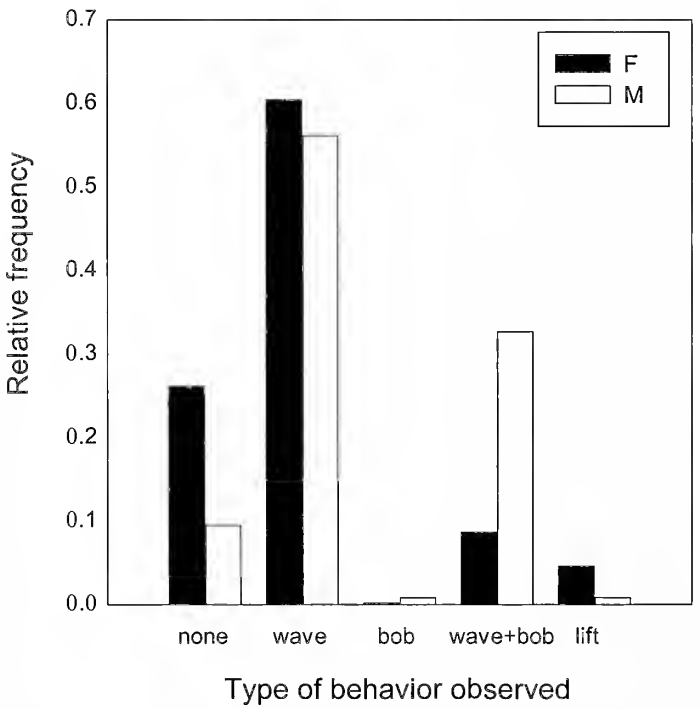

Figure 3.—Relative frequencies of types of behaviors (as described in Table 2) of *Myrmarachne* females and males. Females are represented by the black bars and males by the white bars. (χ^2_4 = 114.07, $P < 0.001$).

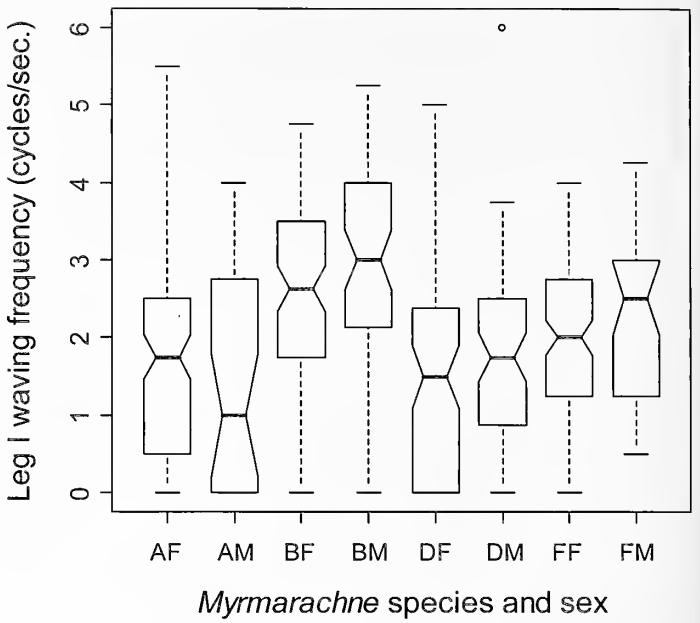

Figure 4.—Notched boxplot of the frequency of leg I waving for each *Myrmarachne* species and sex. Species and sex are coded as: AF = females of species A, AM = males of species A; BF = females of species B, BM = males of species B; DF = females of species D, DM = males of species D; FF = females of species F, FM = males of species F. (ANOVA for species: $F_{(3,57)}$ = 6.41, $P < 0.001$; ANOVA for sex: $F_{(1,57)}$ = 1.10, P = 0.298; ANOVA for species-sex interaction: $F_{(3,57)}$ = 0.56, P = 0.643).

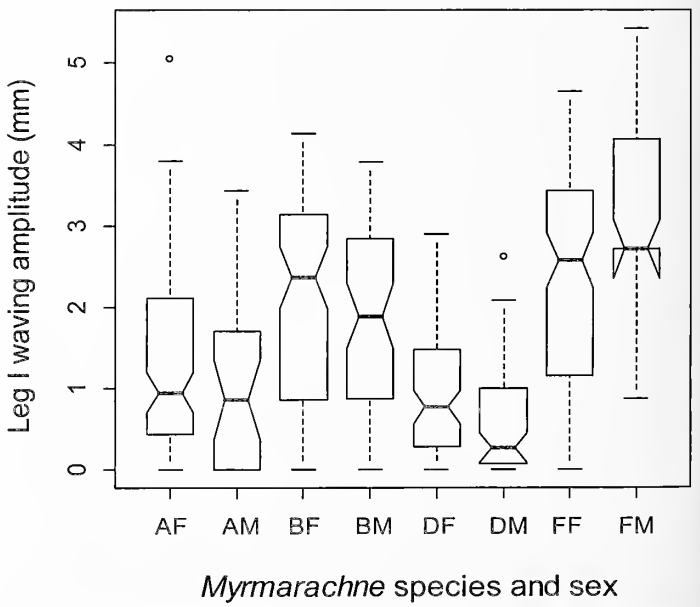

Figure 5.—Notched boxplot of the amplitude of leg I waving for each *Myrmarachne* species and sex. Species and sex coded as: AF = females of species A, AM = males of species A; BF = females of species B, BM = males of species B; DF = females of species D, DM = males of species D; FF = females of species F, FM = males of species F. (ANOVA for species: $F_{(3,57)}$ = 12.20, $P < 0.001$; ANOVA for sex: $F_{(1,57)}$ = 0.005, P = 0.944; ANOVA for species-sex interaction: $F_{(3,57)}$ = 1.63, P = 0.192).

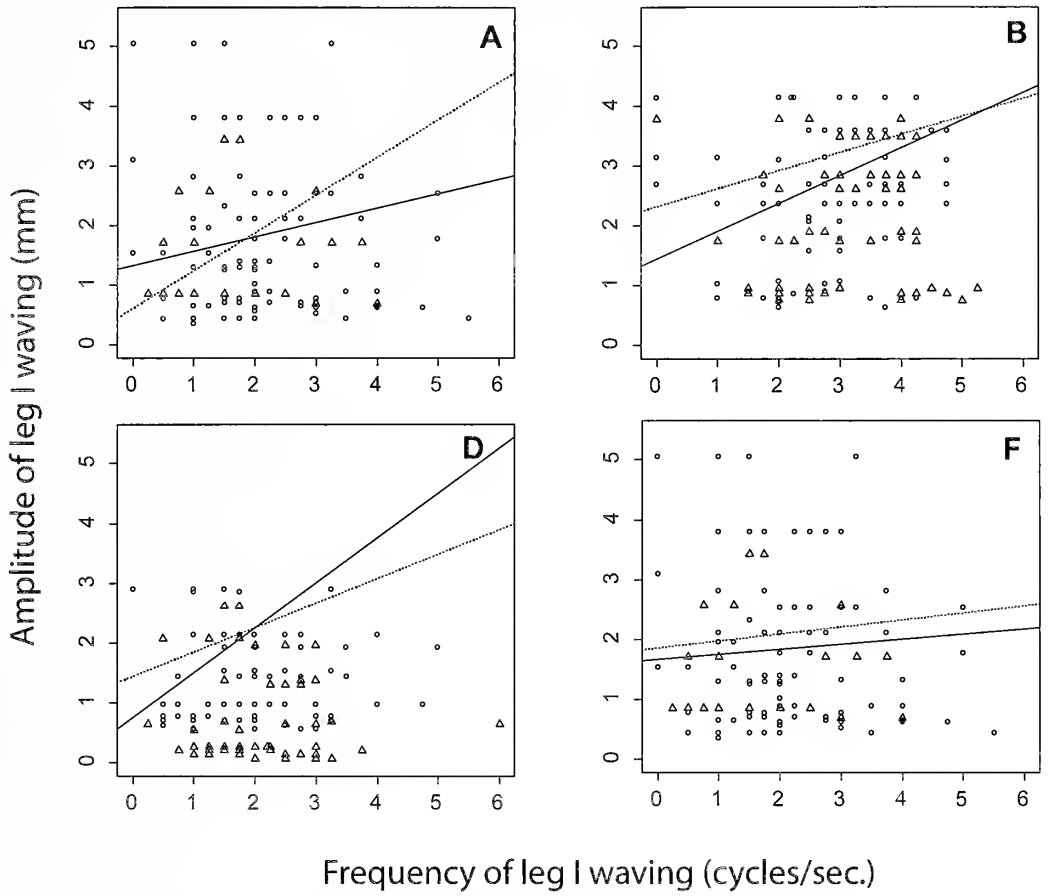

Figure 6.—Scatterplots of frequency of leg I waving (in cycles per second) on the x-axes, versus the amplitude of leg I waving (in mm) on the y-axes for each *Myrmarachne* speeies separately. The species are "A," "B," "D," and "F" as shown on the top right-hand corner of each graph. Data for females is represented by the circles, with the solid best-fit line, whereas data for the males is represented by the triangles and the dashed best-fit line.

running), whether it was bobbing its opisthosoma and whether or not it had the ant in its field of vision (i.e., it was facing the ant with its anterior median eyes). Again, these variables were recorded to find any possible correlations with the leg I movement. This part of the study was also carried out to find interspecific differences in *Myrmarachne* with regard to the average speed and amplitude of the leg waving. The same measurements were recorded for the frequeney (cycles/second) and amplitude of antennal movements in the model ant species.

Data analysis was carried out using the program R version 2.1.1 (R_Development_Core_Team 2005) with the rpart package (Therneau et al. 2005) to build reursive partitioning trees to identify the variables most closely associated with the different groups of antennal illusion and bobbing. Recursive partitioning analysis was popularized by Breiman et al. (1984),

Table 3.—Results of Mantel test for distance matrices of leg/antennal frequency and amplitude for each *Myrmarachne* and ant species. Values shown in table are Mantel's r based on Pearson's product-moment correlation followed by the significance value. Significant correlations ($P < 0.05$) are shown in bold.

	Myrmarachne species			
Ant species	A	B	D	F
Opisthopsis haddoni	**$r = 0.23$**	$r = -0.03$	$r = 0.06$	$r = 0.03$
	$P = 0.002$	$P = 0.676$	$P = 0.089$	$P = 0.299$
Polyrhachis nr. *obtusa*	$r = 0.04$	$r = 0.12$	**$r = 0.11$**	$r = 0.07$
	$P = 0.254$	$P = 0.056$	**$P = 0.012$**	$P = 0.143$
Tetraponera punctulata	$r = -0.01$	$r = 0.07$	$r = -0.01$	**$r = 0.12$**
	$P = 0.517$	$P = 0.106$	$P = 0.564$	**$P = 0.015$**
Oecophylla smaragdina	$r = 0.002$	$r = 0.0007$	$r = 0.06$	$r = 0.07$
	$P = 0.471$	$P = 0.488$	$P = 0.066$	$P = 0.081$

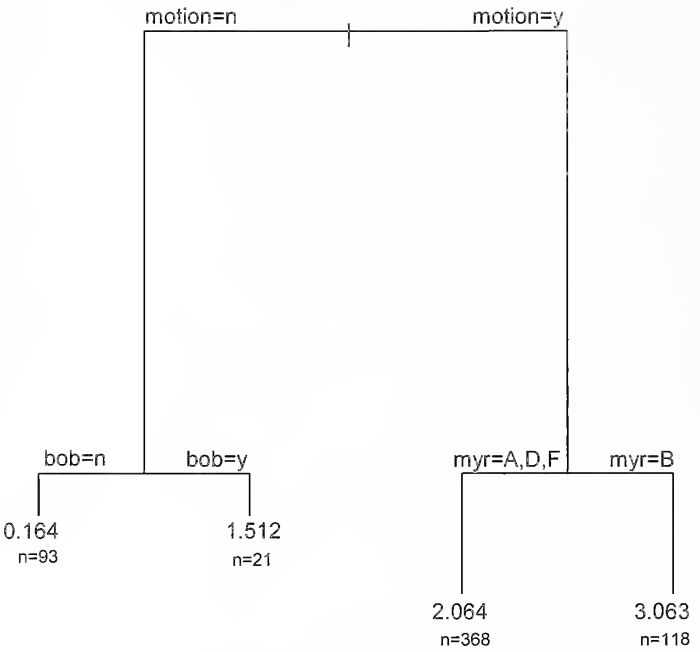

Figure 7.—Recursive partitioning tree of frequency (cycles/second) of leg I waving (values at the end of the branches) by all *Myrmarachne* species, and the variables that are most closely correlated with a particular frequency value. "motion" refers to whether the *Myrmarachne* was moving (y) or not (n), "bob" refers to whether the *Myrmarachne* was moving its opisthosoma up and down (y) or not (n), "myr" is the species of *Myrmarachne* (A, B, D, and F). The letter n at the end of the frequency value represents the number of times that frequency value was placed in correlation with the predictor variables.

and is now widely used in various areas of science (e.g., Lehmann et al. 2003; Karels et al. 2004). This analysis is used to find correlations between mixed (categorical and/or numerical) variables, and the resulting tree shows the dependent variable at the end of the branches and each predictor variable at the nodes. The closer the variable is to the root node of the tree, the higher its predictive value on the outcomes. Repeated measures ANOVA was carried out to determine if there were significant differences in the frequency and amplitude of leg I waving between *Myrmarachne* species and sex. Chi-squared contingency tests were also carried out to find possible differences in behavioral mimicry (count data on the categories described in Table 2) between *Myrmarachne* species and males and females. In addition, a Pearson's correlation test was carried out to find possible correlations between leg I waving frequency and amplitude. This was done to see whether – in the case of a significant correlation – an index of leg I frequency over leg I amplitude could be used as a general measure of leg I movement. Further, Pearson's correlation tests were then carried out to find possible correlations between the leg I movements of *Myrmarachne* species and the antennal movements of their respective model ant species. In case of non-significant results for the Pearson's correlation tests on the leg I/antennal indices, a Mantel's test on distance matrices for frequency and amplitude of model ant antennal movement and *Myrmarachne* leg I movement was also performed on the data.

RESULTS

In this study, when the four *Myrmarachne* species reacted to the presence of ants there was a significant difference in the way they carried out the different behaviors, including the leg I waving (see Fig. 2). *Myrmarachne* species B and D waved their legs I and bobbed their opisthosoma more frequently than species A and F, whereas the latter lifted their legs I without waving more often than species B and D. There was a significant difference between *Myrmarachne* males and females in how frequently they carried out each type of behavior (see Fig. 3). The main difference between males and females was that males bobbed their opisthosoma and waved their first pair of legs more frequently than females.

The frequency (measured in cycles/second) as well as the amplitude of the leg I movement was significantly different between the *Myrmarachne* species but not between *Myrmarachne* males and females (see Figs 4 and 5). There was a positive correlation (Pearson's $r = 0.337$, $P < 0.001$) between the frequency and amplitude of the leg I waving for all *Myrmarachne* species. This correlation gives an indication of the intensity of the movement: the higher up the spider moved its first pair of legs, the quicker it moved them up and down. This trend was consistent throughout all species and both sexes (see Fig. 6). This correlation allowed for the calculation of a general leg and antennal waving index (frequency divided by amplitude).

When the leg waving of each *Myrmarachne* species was compared to the antennal movements of the respective model ants, no significant correlation was found, whether between the frequencies, amplitudes or indices. The Mantel test for leg I waving frequency and amplitude of *Myrmarachne* species versus the antennal waving frequency and amplitude of ant species showed significant correlations between *Myrmarachne* sp. A and *Opisthopsis haddoni*, *Myrmarachne* sp. D and *Polyrhachis* nr. *obtusa*, and *Myrmarachne* sp. D and *Tetraponera punctulata* (see Table 3). There is only one case where a correlation between the antennal movements of the model and the leg I movement of the mimic was found (*Myrmarachne* sp. A and *Opisthopsis haddoni*).

The strongest predictor variable for the frequency of *Myrmarachne*'s leg I waving was found to be whether the spider was moving (walking or running). The species of spider and whether or not the spider was bobbing its opisthosoma were the next most important factors influencing the leg I waving frequency. Thus, the lowest frequencies of leg I waving were most closely correlated with the spider being stationary and not bobbing its opisthosoma. When spiders were walking or running, the higher frequencies of leg I waving were more closely correlated with individuals belonging to *Myrmarachne* sp. B (see Fig. 7). The highest leg I amplitude was correlated most closely with *Myrmarachne* spp. B and F moving (walking or running) whereas the lowest leg I amplitude was correlated with species A and D not moving. The sex of the spider was only a determining factor for leg I amplitude when species B and F were stationary (see Fig. 8).

DISCUSSION

When *Myrmarachne* species reacted to sympatric ants, they commonly waved their first pair of legs, lifting them without the up-and-down movement, and/or "bobbed" their opistho-

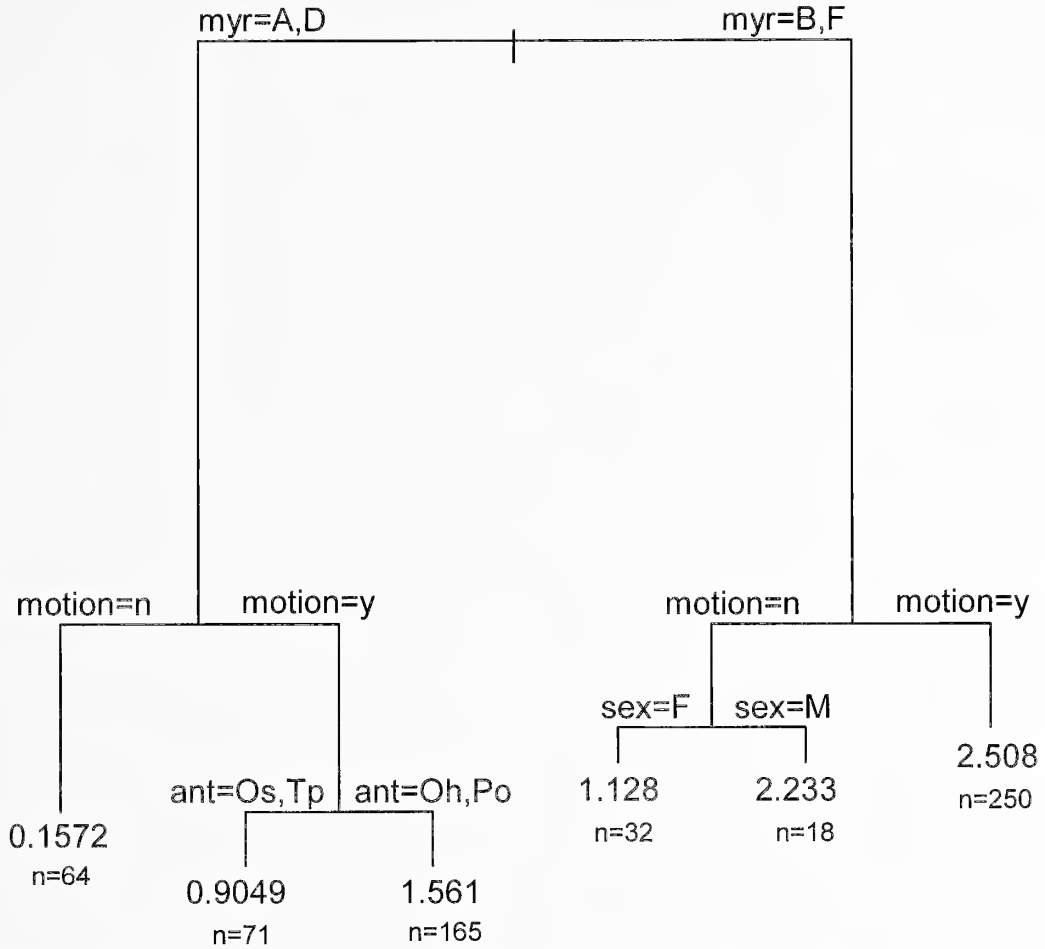

Figure 8.—Recursive partitioning tree of amplitude (in mm, values at the end of the branches) of leg I waving by all *Myrmarachne* species. "Myr" is the species of *Myrmarachne* (A, B, D and F), "motion" refers to whether the *Myrmarachne* was moving (y) or not (n), "sex" is the sex of *Myrmarachne* (M = male, F = female), and "ant" refers to the ant species (Oh = *Opisthopsis haddoni*, Po = *Polyrhachis* nr. *obtusa*, Tp = *Tetraponera punctulata*, Os = *Oecophylla smaragdina*) present in the Petri dish with the spider. The letter n at the end of the amplitude value represents the number of times that amplitude value was placed in correlation with the predictor variables.

soma. This versatile range of behaviors carried out at different frequencies by the four *Myrmarachne* species and between males and females is evidence for behavioral plasticity in these spiders. The up-and-down movement of the opisthosoma - here referred to as "bobbing" - has been observed and commented on before (Jackson 1982) and much resembles the abdominal movements of ants recruiting nest-mates for the defence of the eolony (Hölldobler 1983; Mercier et al. 1997). The lifting of the first pair of legs also resembles the high-held antennae of ants during aggressive displays (Hölldobler 1983; Hölldobler & Wilson 1990). The detailed analysis of the leg waving behavior revealed further interspecific differences in the frequency (or rate, measured as cycles/second) and amplitude with which the *Myrmarachne* species moved their first pair of legs. This motion resembles the antennal movement of ants, yet the leg I waving of each *Myrmarachne* species did not closely match the antennal movements of their respective model ant species. Correlations between the antennal movement of each ant species and the leg I movement of the respective *Myrmarachne* mimic species would have been unrealistic, since there are anatomical and morphological differences between ants' antennae and spiders' legs, and therefore similar movements from these two appendages cannot be expected.

In nature, each *Myrmarachne* species closely associates with an ant species (Edmunds 1978), and the visual similarity of the spider with the ant is striking (Mathew 1954; Jackson 1986). *Myrmarachne* species are Batesian ant mimics, since they do not routinely prey on ants (Jackson 1986; Jackson & Willey 1994), and they are not preyed on as often as non-ant mimics (Edmunds 1993; Nelson et al. 2004; Nelson et al. 2005). The *Myrmarachne* species' leg waving behavior analyzed in this study is likely to be a Batesian mimicry trait, which – like other phenotypic traits in Batesian mimicry – is under strong selection pressure exerted by predation (Mappes & Alatalo 1997). Thus we found interspecific differences and behavioral versatility and plasticity since all these features arise through selection pressure during evolution. The differences between males and females in how often they perform the leg I waving behavior can be explained by the fact that male *Myrmarachne* spiders spend more time exposed to predators when outside their retreats searching for females (Jackson 1982), and must therefore be more convincing mimics than females. In addition, *Myrmarachne* individuals that were walking or

running waved their first pair of legs at a higher rate and amplitude, an observation which is consistent with the hypothesis that the leg I movement complements other ant-like traits when the spider is moving around and therefore more exposed to predators.

Waving the first pair of legs has been observed in several other species of spiders, such as *Habronestes bradleyi* (Pickard-Cambridge 1869) (Allan et al. 1996), *Zodarion germanicum* (Koch 1837) and *Z. rubidium* Simon 1914 (Pekár & Král 2002), and *Sarinda linda* Reiskind (Jackson & Drummond 1974). However the purpose of this leg movement is not the same for all species. In *H. bradleyi*, waving the first pair of legs was found to be a means of detecting alarm pheromones from ants for the spider to prey on (Allan et al. 1996), and in *Zodarion* species it could be a threat display towards the ants (Pekár & Král 2002). Jackson and Drummond (1974) found that males wave their first pair of legs more often than females. So the question arises whether this leg movement is higher in males that are trying to detect female pheromones. However, according to Gaskett (2007) the receptors that detect female pheromones are located on the pedipalps and not on the legs. Furthermore, Nelson and Jackson (2007) showed that *Myrmarachne assimilis* Banks 1930 males use visual, rather than chemical cues to detect the presence of females. Since *Myrmarache* species do not normally prey on ants, and rely on visual rather than chemical cues, waving their first pair of legs is unlikely to be used as a means of detecting airborne chemicals. In the cases where the spiders wave their first pair of legs to mimic the antennal movement of ants, this behavior has been referred to as "antennal illusion" (Reiskind 1977). All the evidence – including the outcomes of this study – support the hypothesis that leg I waving in *Myrmarachne* species is in fact an "antennal illusion," or a trait that has evolved to reinforce the spiders' Batesian ant mimicry.

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Homology in a context dependent predatory behavior in spiders (Araneae)

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Abstract. Stereotyped behaviors have been routinely used as characters for phylogeny inference, but the same cannot be said of the plastic aspects of performance, which routinely are taken as a result of ecological processes. In this paper we examine the evolution of one of these plastic behavioral phenotypes, thus fostering a bridge between ecological and evolutionary processes. Foraging behavior in spiders is context dependent in many aspects, since it varies with prey type and size, spider nutritional and developmental state, previous experience and, in webweavers, is dependent on the structure of the web. Reeling is a predatory tactic typical of cobweb weavers (Theridiidae), in which the spider moves the prey toward her by pulling the capture thread (gumfoot) to which it is adhered. Predatory reeling is dependent on the gumfoot for its expression, and has not been previously reported in orbweavers. In order to investigate the evolution of this web dependent behavior, we built artificial, pseudogumfoot lines in orbwebs and registered parameters of the predatory tactics in this modified web. Aspects of the predatory tactics of 240 individuals (12 species in 4 families) were measured, and the resulting data were optimized on the phylogeny of Orbiculariae. All species perform predatory reeling with the pseudogumfoot lines. Thus, predatory reeling is homologous for the whole Orbiculariae group. In nature, holes made by insects in ecribellate orbs produce pseudogumfoot lines (similar to our experimentally modified webs), and thus reeling occurred naturally in ecribellates. Nevertheless, outside lab conditions, predatory reeling does not occur among cribellate orbweavers, so that this behavior could not have been selected for in the cribellate ancester of orbweavers. Cribellate spiders are flexible enough as to present novel and adaptive predatory responses (reeling) even when exposed for the first time to conditions outside their usual environment. Thus, the evolution of reeling suggests an alternative mechanism for the production of evolutionary novelties; that is, the exploration of unusual ecological conditions and of the regular effects these abnormal conditions have on phenotype expression.

Keywords: Behavior, evolution, orbweb, gumfoot, predatory sequence

Although stereotyped behaviors have been routinely used as a basis for phylogenetic inference in spider literature (Eberhard 1982; Coddington 1986; Griswold et al. 1998; Kuntner et al. 2007), the same is not true of the plastic aspects of performance, those dependent on context for their expression. Plasticity refers to learning (Pigliucci 2001) or, more generally, to aspects of performance that vary with the context of its occurrence, such as variability of the predatory sequence as a function of the kind and size of prey (Robinson 1975; Li 2000; Garcia & Japyassú 2005), or variability in web parameters as a function of the presence of specific prey (Sandoval 1994) or the presence of predators (Li & Lee 2004). The logic underlying the use of stereotyped behaviors for phylogeny estimation is the same as that underlying the use of morphological data: stereotyped behaviors are as species typical as morphology, and it has been shown that there is no significant difference between those two kinds of data in assessing phylogeny (de Queiroz & Wimberger 1993). Although the same may not be true of the plastic aspects of performance, because of its closer connection to environmental factors, even these plastic aspects of behavior can be subjected to selection (Daly et al. 1982). These more complex behavioral phenomena could reveal details of a more intricate evolutionary process, one with simultaneous competing selection pressures, besides providing a richer database for extracting phylogenetic patterns (Japyassú & Viera 2002). Also, the ability to make plastic adjustments varies among taxonomic groups and this ability could itself provide useful characters for phylogenetic analyses (Japyassú & Caires 2008).

As an example of the evolutionary intricacies that context dependency can unravel, we focus here on the evolution of a putative behavioral synapomorphy of cobweb spiders (Theridiidae): a typical attack tactic named reeling. Most theridiid webs have gumfoot lines or lines with glue droplets spread all over (Benjamin & Zschokke 2003). These special capture threads extend from a structural net (where the spider rests) to the substrate. Prey items adhere to the gumfoot, and then the spider walks under its sheet/net to touch this capture line, which it reels in with alternate movements of its front legs (while legs III roll up the capture line producing a silken pellet), bringing the prey close enough to be wrapped with viscid silk. If the prey has escaped from the gumfoot and is walking nearby, the spider can walk down the gumfoot and leave the web, walking over the ground searching for the prey (Japyassú & Jotta 2005; Garcia & Japyassú 2005).

Reeling and the other behaviors related to gumfoot lines (such as the above described sticky silk wrapping and ground search, as well as gumfoot line building) have also been observed in a phylogenetically distant family (Pholcidae, Japyassú & Macagnan 2004). The homoplasious co-occur-

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rence of this potentially independent set of behaviors suggests that they somehow require one another, that together they form a complex adaptation. Since these behaviors are all related to a single web structure, the gumfoot, it is tempting to think that gumfoot evolution could facilitate the appearance of the other associated behaviors, that gumfoot lines could somehow function as a stimulus to the oceurrence of those units of predatory behavior. Predatory behavior is overtly context dependent (Robinson & Olazarri 1971; Coddington & Sobrevila 1987; Edwards & Jackson 1993, 1994; Jackson & Wileox 1993; Jackson & Pollard 1996; Japyassú & Viera 2002; Japyassú & Jotta 2005), and the web is the most immediate context for its expression. So, it is not unreasonable to suppose that the evolutionary appearance of web structures (gumfoot lines) could lead to abrupt changes in web-based behaviors. In the present paper we comparatively explore this possibility, experimentally manipulating the context (web) of predatory performance in a number of spider families related to cobweb weavers (Theridiidae). Since the Orbiculariae outgroups of theridioids (Theridiidae + Nesticidae), namely linyphioids (Linyphiidae + Pimoidae) and orbweavers, do not build gumfoot lines (Benjamin & Zschokke 2003, 2004), we have created "gumfoots" in the orbwebs in order to register possible new predatory behaviors occurring in this new, artificial web context.

We use this experimental, comparative data, to understand the evolution of a context dependent behavior (predatory reeling), plotting its occurrence (in this modified web context) on the phylogeny of the group. We also discuss the implications of these results for the evolution of context dependent behaviors in general.

METHODS

Artificial gumfoot lines (pseudogumfoot lines) were produced in orbwebs (see below), and the predatory behavior on these modified webs was compared to that performed on naturally gumfooted theridiid webs. Spider species were chosen for their abundance, phylogenetic position, and possibility of web manipulation. Twelve species distributed in four families were included in the analysis, eaeh comprising 20 adult females (each spider was observed for only one predatory sequence). The orbweavers *Zosis geniculata* (Olivier 1789) (Uloboridae), *Micrathena nigrichelis* Strand 1908, *Alpaida veniliae* (Keyserling 1865), *Metazygia rogenhoferi* (Keyserling 1878), *Metazygia gregalis* (O. Pickard-Cambridge 1889) (Araneidae), and two unidentified *Leucauge* species (Tetragnathidae) were observed in this study. Information about five species of cobweavers (Theridiidae) was extracted from previous studies in the lab (see below). Spiders were collected at various remnants of Atlantic forests in São Paulo city (Brazil): reserve of the São Paulo University ("Armando Salles Oliveira", CUASO, 23°33′S, 46°43′W), Morro Grande reserve (Cotia, 23°40′60″S, 47°01′60″W), Ilha dos Eucaliptos (island in Guarapiranga reservoir, 23°43′59.90″S, 46°44′02.53″W), Parelheiros (area on the edge of the Guarapiranga reservoir, 23°43′58.86″S, 46°44′27.27″W), Guarapiranga Park (23°40′28.54″S, 46°43′55.39″W) and Oswaldo Cruz Park (Instituto Butantan, 23°33′S, 46°43′W). Voucher specimens were deposited in the arachnological collection at Instituto Butantan (IB57626–46, IB57434–42, IB57392–99 e IB 57560–88; curator A.D. Brescovit).

For each specimen, we observed the predatory behavior until the first contact with the prey (*Gryllus* sp, of the same size as the spider — cephalothorax + abdomen). We measured the displacement (cm) of the spider and/or of the prey (through reeling) in the gumfoot (or pseudogumfoot) for each specimen and expressed this measure as a percent of the total capture thread length [reeling extent (RE)]. We considered that the spider reeled if the prey was displaced as a result of alternate movements of the front legs pulling the capture line.

The spider predatory behavior was separated into two categories: definite or mixed responses. In definite responses the spider could either entirely reel in the (pseudo)gumfoot (i.e., standing at the hub, the spider pulled in the entire gumfoot line with her front legs, until she touched the prey, RE = 100) or she could not reel it in at all, walking from the hub to the prey along the capture line (RE = 0). In the mixed responses the spiders first walked along the length of the capture line and then initiated reeling movements ($0 < RE < 100$).

Web context manipulation.—Pseudogumfoot lines were produced in the orbwebs of spiders from three families (Uloboridae, Araneidae, and Tetragnathidae). For our purposes, the main difference between a real gumfoot line in a cobweb and a radius in an orbweb is that the gumfoot is easily detached from its point of attachment on the substrate (through reeling), while the radius is firmly attached to the frame of the orb (forbidding the execution of reeling). Thus, in order to make a radius more similar to a gumfoot, we simply cut it at the midpoint from the hub to the frame. This loose radius was ealled a pseudogumfoot. The prey was then left at the free end of this pseudogumfoot (Fig. 1a). The radius selected for this procedure was always in the lower portion of the webs, in the middle of an intact sector of the orb.

This procedure was modified in the web of the cribellate *Z. geniculata*. The adhesive spiral in cribellate webs is less extensible than in the ecribellate ones (Kölher & Vollrath 1995). Thus, even with a free end, the cut radius (pseudogumfoot) was still firmly connected to the rest of the trap through a bunch of poorly extensible, cribellate adhesive spiral threads that prevented reeling. In order to overcome this difficulty, we freed this radius even more, also cutting all the adhesive spiral threads except for the most peripheral one (Fig. 1b).

We have not succeeded in producing similar pseudogumfoot lines in the web of the linyphiid *Dubiaranea* sp., because her trap is composed of a horizontal sheet of densely interwoven threads with nothing similar to radii or spirals. We have tried to make *Dubiaranea* sp. specimens adopt the web of other species (for example, theridiid webs), but again we did not succeed. As a result, we could not include linyphiids in the sample.

The theridiids used in this study build gumfoot lines naturally, so no experimental manipulation was necessary (Fig. 1c). The predatory behavior of the theridiids included in this analysis is well doeumented. We took the data from videotapes of predatory sequences of 20 adult females of each of the following species: *Achaearanea cinnabarina* Levi 1963 (Japyassú & Jotta 2005), *Latrodectus geometricus* C.L. Koch 1841 (Corrêa & Japyassú 2001), *Achaearanea digitus* Buckup & Marques 2006 (Japyassú & Caires 2008), *Achaearanea tepidariorum* (C.L. Koch 1841) (Macagnan & Japyassú,

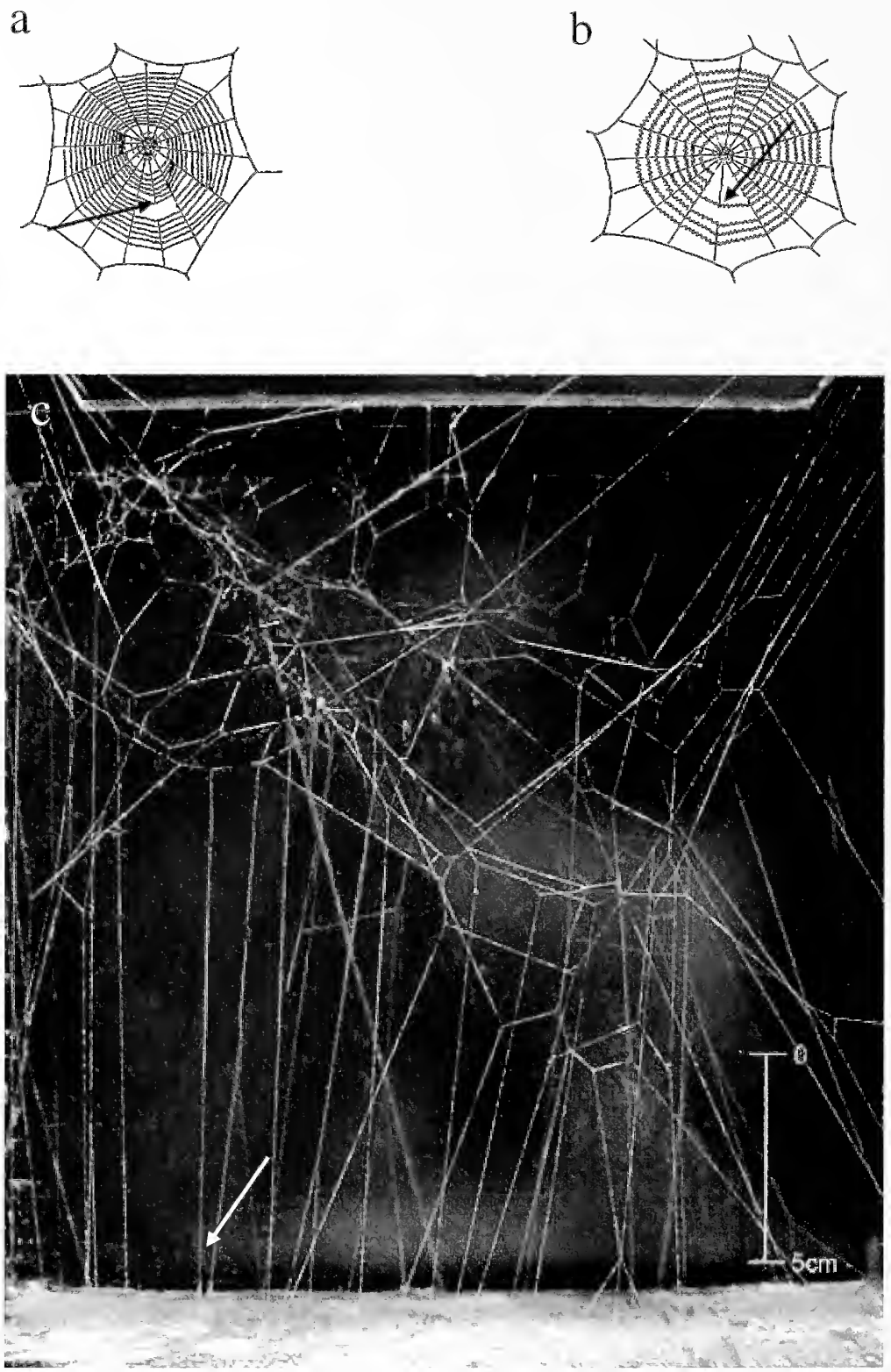

Figure 1.—Pseudogumfoot and gumfoot lines. Pseudogumfoot lines were produced through two different procedures. For ecribellate spiders [Araneidae (*Micratena nigrichelis*, *Alpaida veniliae*, *Metazygia rogenhoferi*, and *Metazygia gregalis*) and Tetragnathidae (two unidentified *Leucauge* species)] a radius was cut in its midpoint (a). For cribellate spiders [Uloboridae (*Zosis geniculata*)] adhesive spirals connected to the freed radius were also cut (b). Webs of theridiids (in the photo, web of *T. evexum*, other species used include *Latrodectus geometricus*, *Achaearanea cinnabarina*, *Achaearanea digitus*, and *Achaearanea tepidariorum*) do present gumfoot lines in natural conditions. The gumfoot lines are the vertical lines connecting the upper sheet to the substrate (c). Arrows point to the place where prey was introduced in the manipulated webs.

Table 1.—Percent of spider responses and mean reeling extent (RE) in the species studied.

Family	Species	RE	Spider responses		
			Full reeling	No reeling	Mixed
Uloboridae	*Z. geniculata*	59.9	2	9	9
Araneidae	*M. nigrichelis*	48.5	2	9	9
	A. veniliae	31.5	0	12	8
	M. rogenhoferi	51.9	0	14	6
	M. gregalis	29.0	0	18	2
Tetragnathidae	*Leucauge* sp 1	61.6	5	7	8
	Leucauge sp 2	41.2	0	13	7
Theridiidae	*L. geometricus*	82.9	6	8	6
	T. evexum	28.1	0	18	2
	A. cinnabarina	52.8	2	10	8
	A. tepidariorum	100.0	2	18	0
	A. digitus	87.6	13	2	5

unpublished data) and *Theridion evexum* Keyserling 1884 (Garcia & Japyassú 2005).

Phylogenetic analysis.—We used the phylogeny of Griswold et al. (1998) modified at the araneid (Scharff & Coddington 1997) and theridiid (Agnarsson 2004) nodes to reflect the internal relationships within these families. The occurrence, frequency, and degree of predatory reeling in each species was plotted and optimized over the species phylogeny using the software package Mesquite (version 2.0). The ancestral states for the continuous characters were reconstructed with the parsimony method. Since the linear parsimony model does not apply to phylogenies with polytomies, we used the squared parsimony model instead (Maddison & Maddison 2006).

RESULTS

Reeling during the predatory sequence occurred in all species included in the analysis. In all species the spiders touched the gumfoot (theridiids) or the pseudogumfoot (orbweavers) and pulled it with alternate movements of their front legs. In a typical cycle of leg movements, the right leg I was pulled to the cephalothorax, holding the capture line until the next leg (left, II) grasped it, when leg I (right) was put forward, while leg II (left) was pulled to the cephalothorax; this sequenee passed orderly through the front legs (I right, II left, I left, II right) only to repeat itself as a cycle until the spider touched the prey hanging on the capture thread. *Zosis geniculata* (Uloboridae) sometimes performed this sequence slowly, so that we could observe that legs III rolled up the capture line (i.e., the experimentally broken radius) as the front legs pulled it, producing a silk pellet as a result. This cycle occurred in all species observed, so this coordination of leg movements, used precisely in the context of prey capture, optimizes at the base of the phylogeny of the whole Orbiculariae group.

We also observed orbwebs that had naturally occurring pseudogumfoot lines, that is, radii that were naturally broken, probably due to the activity of insects, or due to previous prey captures, which resulted in small holes in the orbweb. One of us (CRMG) observed *M. rogenhoferi* (Araneidae) capturing prey ensnared in these naturally broken radii with reeling movements. Although we have also found naturally occurring holes in webs of *Z. geniculata*, these spiders never reeled the prey we offered at the end of the naturally broken radius. It seems that the cribellate adhesive threads form a strong and resistant net with the broken radius, inhibiting the spider from pulling the broken radius with reeling movements. Thus, in our sample, reeling occurs naturally among ecribellate, but not among cribellate orbweavers.

Although all species showed reeling, there was considerable variation among them. The mean extent of reeling (RE) varied in such a way that we could not detect any tendency of increase or decrease of it along the phylogeny (Table 1).

We plotted the degree of mixed responses (the number of individuals with mixed responses, i.e., of spiders that both walked to the prey and reeled the gumfoot in one single predatory bout) on the phylogeny of the clade Orbiculariae. The results clearly indicate that the degree of mixed responses decreases from the root to the tip of the phylogeny. All but one of the state transitions, from ancestral to derived clades, is from a higher to a lower number of mixed responses (Fig. 2). The evolutionary reduction in mixedness occurs independently in two clades: once inside the family Araneidae and again inside the clade subtending Tetragnathidae and Theridiidae. Among araneids the frequency of mixed responses decreases only in favor of the tactic "no reeling," while in the theridiid lineage, it decreases sometimes in favor of "no reeling" (as in *T. evexum*) and sometimes in favor of "full reeling" (as in *A. digitus*, Table 1).

DISCUSSION

Reeling web threads to capture prey is homologous for all orbweavers. It occurs even in the outgroup of Araneoidea (*Z. geniculata*) when an adequate context (an artificially manipulated web, with a pseudogumfoot - i.e., a loose radius) is present. *Zosis geniculata* (Uloboridae) performs, in all detail, the long coordination of alternate movements of the front legs, exhibiting even full reeling; e.g., it performs a sequence in which the spider starts reeling movements at the hub (where she rests), and stops only when she touches the prey, still at the hub. The predatory reeling of orbweavers (described for the first time in the present paper) is homologous to the previously described theridiid reeling (see, for example, Garcia & Japyassú 2005), because it is used at the same moment in the capture sequence (after detection and before biting the prey), with the same topology of leg movements and with the same function, fulfilling the traditional criteria for primary

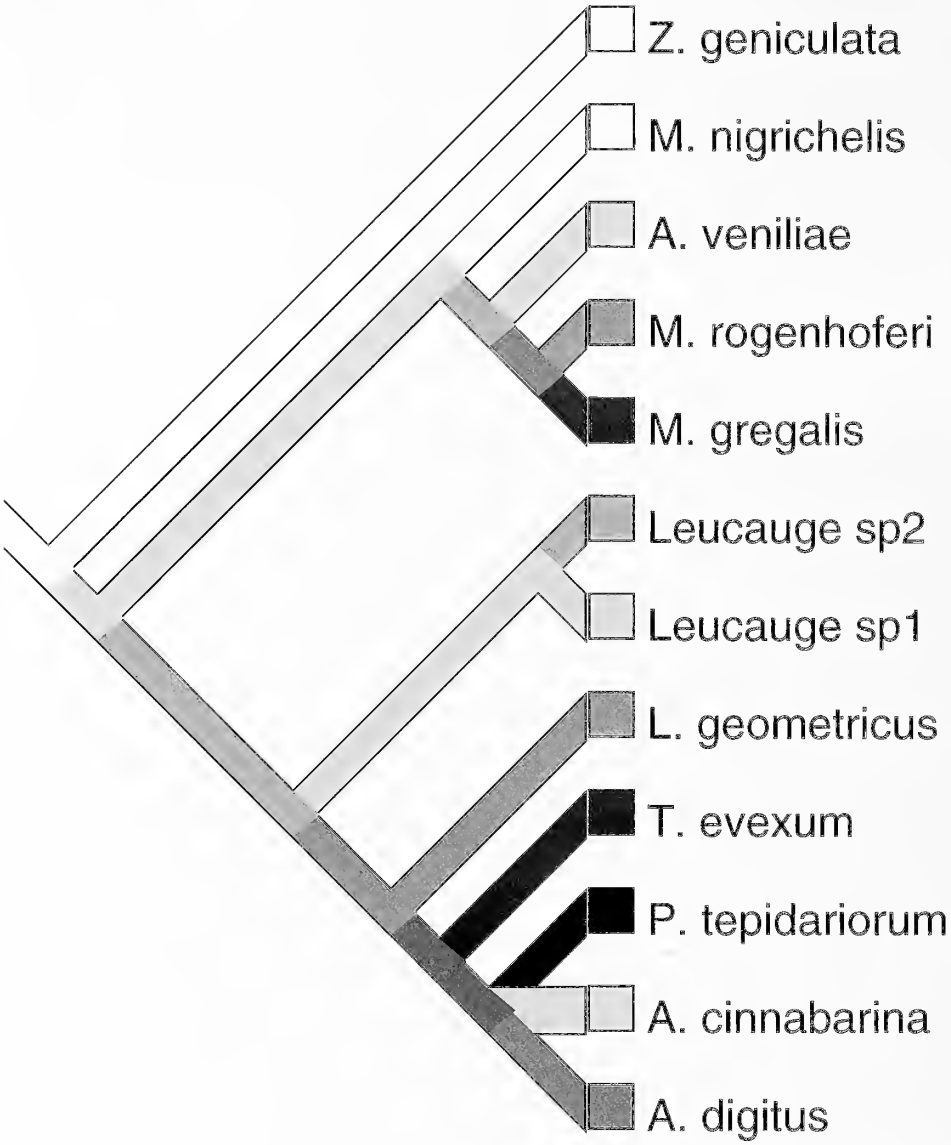

Figure 2.—Evolution of predatory reeling in the clade Orbiculariae. Whiter colors means higher number of mixed responses in the taxon (higher number of individuals performing mixed responses). The number of individuals with mixed responses (i.e., of spiders that both walk to the prey and reel the capture line in a single predatory bout) decreases from ancestral to derived clades.

homology (Wenzel 1992). Also, predatory reeling is congruent with the majority of the other characters used to estimate the phylogeny of the group, since it perfectly fits the phylogeny of Orbiculariae, thus standing also as a secondary homology statement (sensu de Pinna 1991). This should be considered as a provisional (secondary) homology statement since we presently have data for only a few species of orbweavers. Nevertheless, we are confident that reeling will still be homologous when additional species are examined. We have observed other species (not included in the analysis because of the small number of individuals or lack of complete identification), such as the araneids *Acacesia* sp. (2 young specimens), *Araneus* sp. (4 adults), *Eustala* sp. (2 adults, 4 young), *Mangora* sp. (4 adults, 2 young), *Parawixia* sp. (4 young) *Verrucosa* sp. (1 adult), *Gasteracantha cancriformis* (10 adults), *Wagneriana* sp. (1 adult), and also *Tetragnatha* sp. (Tetragnathidae, 6 adults, 4 young); in all of them reeling was present. Reeling occurred even among young spiders in all species whereupon it was tested (including exemplars of *A. veniliae* and *Leucauge* sp., included in our analysis); an indication that previous experience could be unnecessary for the display of this behavior. Thus, it seems to us that the presence of predatory reeling is strongly supported as a basal feature of Orbiculariae.

Although predatory reeling is a basal feature of Orbiculariae, uloborids (one of the basal groups of Orbiculariae) do not perform it unless we offer them modified webs with pseudogumfoot lines. This is probably a consequence of the cribellate adhesive spiral, a thread that is tough enough to keep the radii firmly in place even when a radius is broken. Thus, the occurrence of predatory reeling in nature is precluded by the very nature of the cribellate adhesive thread. Since predatory reeling does not occur naturally in uloborids, it cannot have been selected for during the evolution of these spiders simply because any trait needs to be at least expressed in order to be selected. Nevertheless, among ecribellate

orbweavers it is expressed, albeit occasionally, in natural conditions: some radii are unpredictably broken by struggling prey that leave holes in the webs, and these broken radii stand as natural pseudogumfoot lines (since the viscid spirals connect the broken radius loosely to the web). So, it seems that the appearance of the viscid, more extensible ecribellate adhesive thread (Kölher & Vollrath 1995) has exposed to selection an old but until now unexpressed coordination of leg movements: predatory reeling. Finally, among theridiids, predatory reeling seems to have evolved into a specialized capture tactie, associated with a specialized web structure, the gumfoot.

Although predatory reeling was "present" long before being expressed, it seems that the actual expression of it had an impact on its evolution since the level of mixed responses reduces progressively after its first expression at the base of Araneoidea (Fig. 2). More direct responses, that is, full reeling or full locomotion (of the spider) to prey (instead of a mix of both responses), could be selected for, being quicker or more efficient in subduing the prey, but at the moment we have no data to help tease apart these possibilities. What seems clear is that, in order to have a more direct response, the spider needs to know earlier which tactic to employ in the capture sequence: to move the prey towards herself (full reeling), or to move herself towards the prey. The spider needs to evaluate the situation before making the first move. Thus, more direct responses imply the evolution of some kind of decision-making mechanism in order for the spider to get the information necessary to opt between the two competing tactics as early as possible.

The strong variability in the extent of reeling (RE) among species (Table 1) could be due to differences in starvation. Spiders well fed are more selective as to prey type (Li 2000), so it is possible that feeding condition affects other foraging responses. Nevertheless, this does not seem to be the case because previous results demonstrate that differences in starvation do not affect parameters of predatory reeling (Gonçalves et al. 2006). This variability is probably tied to some ecological condition we did not evaluate.

Origins of reeling outside the predatory context.—Although predatory reeling is a novelty for orbweavers, these spiders do perform reeling movements outside of a predatory context. While building the radii of their orbwebs, spiders from the family Uloboridae (Wiehle 1927; Eberhard 1972, 1990), Araneidae (Peters 1933; Tilquin 1942, p. 195; Eberhard 1982, 1990), Tetragnathidae, Theridiosomatidae, and Anapidae (Eberhard 1982) cut and reel a temporary radius upon laying a permanent one. Theridiids like *Achaearanea tepidariorum* and *Latrodectus geometricus* (Eberhard pers. comm.) also maintain this behavior while building the gumfoot lines of their cobwebs. In another example of reeling, orbweavers that are hanging on a dragline, climb back up it with reeling movements of the front legs, while legs III make a pellet from the dragline (Tilquin 1942, pp. 116–125). Orbweavers also cut and reel threads upon building a silken bridge between two points in order to make the web below it (Tilquin 1942, pp. 140–142). This bridging behavior is also common among non-orbweavers (Deeleman 2007), which make bridges in order to walk from one place to another in the vegetation.

Thus, there are several kinds of reeling among orbweavers, and it is possible that all of them compose a single character with multiple states. If this is the case, predatory reeling could be still another state of this compound character, but at the moment we have no data to support this hypothesis.

Implications for the evolution of context dependent behaviors.—Our results point to an evolutionary path that starts with a behavior that cannot be a predatory adaptation (since it is not expressed in predatory events), one that is later exposed to selection via evolutionary changes in the context (ecribelate orbweb) of its expression, and finally, through further changes in this context (gumfoots of cobwebs), beeome an adaptation. The evolution of this new prey capture tactic (reeling) did not result from the evolution of any new coordination of motor actions. The coordination of the movements needed to reel the prey was already in place when it was first expressed with a predatory function. Instead, reeling required the evolution of an adequate environment, or context, for its appearance (a pseudogumfoot, i.e., a loose radius). To our knowledge, this is the first report of an evolutionary change due to a change in the eontext of expression of the trait, not to a change in the trait itself.

There is abundant literature on the evolution of one behavioral trait as a response to the previous evolution of other behavioral traits; more precisely, as a response to the extraorganismal effects of these previous behavioral traits. Odling-Smee et al. (2003) extensively review this literature, naming these behaviors (with extraorganismal effects) niche-construction, and they argue for a kind of pleiotropic connection between the two behavioral traits, a conneetion that is mediated by the external effects (the "extended phenotype") of the ancestral behavioral trait. This niche-construction perspective certainly grants evolutionary power to the context of occurrence of a behavior with non trivial outcomes such as the maintenance of polymorphic equilibria, or even the fixation of otherwise unfavored alleles [see Odling-Smee et al. (2003) for the results of different evolutionary simulations under different modeling assumptions, pp. 133–166], but in the present paper we are not dealing with niehe construction but with a different phenomenon.

In all niche-construction models a niche-constructing behavior (such as nest construction among *Gasterosteous* or cichlids) alters the environment, and this new environment acts as a selection pressure for the appearance of other, derived behaviors (such as elaborate courtship rituals in the examples above - McLennan et al. 1988, Odling-Smee et al. p. 95). In the case of predatory reeling, we are dealing with an instantaneous event: *Z. geniculata* never uses predatory reeling in nature, but if you provide an artificially modified web (with a loose radius) she immediately uses this new behavior. So, there is no time for selection to mold this new predatory tactic (reeling), which is simply a result of a plastic behavioral system exposed to unexpected conditions. It is only after reeling appears regularly in the repertoire of orbweavers (after the loss of the cribellum among Araneoidea), that selective forces can help to mold this new tactic.

This should not be considered an unusual, but rather an unexplored evolutionary scenario. Studies show that spiders can behave in atypical ways when subjected to atypical conditions. Gundermann et al. (1993) observed unusual social

behavior in a typically solitary species when the spiders were forced to live under unusually high densities. Roland et al. (1996) show that maternal behavior can be induced experimentally outside its normal conditions of occurrence. These phenomena fall into the general category of behavioral plasticity, but in these cases we are dealing with the study of plasticity outside the normal range of the species' ecological conditions, outside the normal population density, outside normal conditions for maternal care, or outside the normal web conditions (present study). Thus, the evolution of reeling suggests a new mechanism for the production of evolutionary novelties, that is, the exploration of unusual ecological conditions and of the regular effects that these abnormal conditions have on phenotype expression.

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Trechona rufa (Araneae, Dipluridae): new status, redescription and neotype designation with notes on the genus

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Abstract. In this paper, *Trechona venosa rufa* Vellard 1924 is elevated to species rank, a neotype is designated, the male is described for the first time, and the female is redescribed. *Trechona rufa* seems to be restricted to the Atlantic Forest of São Paulo state, southeastern Brazil, covering an area along the coast and going up to the southern slope of the Mantiqueira mountain chain. The composition and distribution of the genus *Trechona* is changed. As a result, only three valid species remain in *Trechona*, all inhabiting the Atlantic Forest of Brazil. The other species formerly included in *Trechona* are considered below: *T. lycosiformis* (C.L. Koch 1842) = *Avicularia lycosiformis* comb. nov., Theraphosidae *incertae sedis*; *T. sericata* (Karsch 1879) = *Linothele sericata* (Karsch 1879), Dipluridae *incertae sedis*; *T. adspersa* Bertkau 1880 = Nemesiidae incertae sedis; *T. rogenhoferi* (Ausserer 1871) = *nomen dubium*.

Keywords: Taxonomy, Brazil, Neotropics, Atlantic Forest, Mygalomorphae

The genus *Trechona* Koch 1850 includes spiders with a body size up to 50 mm. The genus may be recognized by the well developed lyra on the internal side of the pedipalp maxilla. This stridulating apparatus (Raven 1985:fig. 30) is formed by numerous rigid setae, sorted in two size classes: approximately 15–20 mm long, robust setae, placed in one wide series (the middle setae are the longest and strongest ones, bearing a distinctly club-shaped apex on each one), and 50 or more shorter, thinner setae, disposed in several smaller series. The shorter setae are placed posteriorly to and cover most of the extension of the series of longer setae, forming a large black to reddish brown setal plate. This setal plate is strikingly different from the single series of up to 10–20 clavate setae found in the known species of *Diplura* Koch 1850 (Raven 1985:fig. 20). Excepting *Diplura*, the other diplurids lack lyra (Raven 1985). In *Trechona*, the setae of the lyra are probably rubbed against the pecten, formed by 6–9 strong, erect setae placed at the outer, basal margin of the chelicera. Adult *Trechona* have a brownish to black coloration, usually forming transverse light stripes (zebra pattern) on the dorsum of the abdomen. Currently, six species and one subspecies are included in *Trechona*, distributed from Brazil to Guyana and Colombia (Platnick 2008).

Vellard (1924) redescribed the female of *T. venosa* (Latreille 1832), based on several specimens from Rio de Janeiro and Niterói, both localities in Rio de Janeiro state. He described an additional male he attributed to *T. venosa* based on a specimen from Fortaleza de Minas, Minas Gerais state. In the same paper, he briefly described *T. venosa rufa* Vellard 1924, a new subspecies with lighter coloration than *T. venosa venosa*, based on the female holotype from Cubatão, São Paulo state (and not a male holotype as misprinted in Pedroso & Baptista 2004). In the same paper, Vellard also cited two additional females of *T. v. rufa* from unknown localities in the same state. Bücherl (1957) claimed that the status of *T. v. rufa* as a separate subspecies was doubtful, as he considered its somatic and genital characteristics as identical to those of *T. v. venosa*. Nonetheless, he cautioned that the limited number of available specimens did not allow a sound decision on the division of *T. venosa* into subspecies. Pedroso & Baptista (2004) redescribed *T. venosa venosa* and pointed out that *T. v. rufa* was probably a separate species. However, they did not formally elevate *T. v. rufa* to species rank as more specimens were needed to clearly separate both species and to establish the boundaries between their geographic distributions.

This paper aims to redescribe *Trechona rufa*, raise it to species rank, designate a neotype and describe the male for the first time. We also wish to throw some light on the tangled taxonomy and distribution of the genus *Trechona*.

METHODS

The color pattern was based in specimens preserved in 75% ethanol, supplemented by information based on living specimens. Measurements and illustrations were made with a Wild Heerbrugg M8 stereoscopic microscope, camera lucida, and micrometric eye-piece. Measurements are given in millimeters. Cephalothorax length was measured from the posterior border of the cephalothorax to the anterior margin of the chelicerae. Total length was measured from the posterior border of the anal tubercle to the anterior margin of the chelicerae, not including the spinnerets. Each article of the pedipalp and the first leg was measured in retrolateral view, from the basal condylus to the distal one. The number of specimens measured is given in parentheses, followed by the modal value and by the range of variation in parentheses. The distribution map was elaborated through the use of geographical coordinates obtained from Global Gazetteer version 2.1 (Online at http://www.fallingrain.com/world, last accessed 20 October 2007).

As usual, the vulva was examined through dissection of the genital region of the females. The piece containing the vulva was then cleaned and immersed in a proteolytic enzyme

solution (Prolase 300) for 24 hours. After clearing, a temporary mounting of the vulva was made using glycerol gel and an excavated glass slide.

Abbreviations used: IBSP - Instituto Butantan, São Paulo, Brazil; IRSNB – Institut Royal de Sciences Naturelles de Belgique; MNRJ - Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. FIOCRUZ – Fundação Oswaldo Cruz, Rio de Janeiro, Brazil; ZMHB – Zoologisches Museum, Humboldt Universität, Berlin, Germany. Additional information and color pictures of *Trechona* are available on our website: http://www.museunacional.ufrj.br/mndi/Aracnologia/Trechona.htm.

TAXONOMY

Trechona C.L. Koch 1850

Mygale Lamarck 1802 (in part)
Onysopelma Simon 1864:68; Ausserer 1871:197 (synonym)
Pezionyx Simon 1864:530, 538 (*nomen superfluum* for *Onysopelma*)
Eudiplura Simon 1892:179; Raven 1985:75 (synonym)

As noted in the Introduction, Raven (1985) stated that there are up to 10 clavate setae in the known species of *Diplura* Koch 1850, arranged in a single series. However, we have examined specimens of several *Diplura* species, including undescribed ones, with a higher number of setae (14, 15, and up to 20). It follows that the most useful character to diagnose species of *Trechona* and *Diplura* in relation to the lyra is not the number of large setae but the presence in *Trechona* of several series of clavate setae arranged in a plate, with the first series composed of much larger clavate setae than the other ones (compare Raven 1985, figs. 20 and 30)

As the preliminary results of our ongoing work on *Trechona* suggest, the genus composition and distribution need thorough revision. Most *Trechona* species now considered as valid are herein transferred to other genera and families or suffer a change in status.

Trechona rufa Vellard 1924 new status
(Figs. 1–9)

Trechona venosa rufa Vellard 1924:157.
Trechona venosa rufa: Bücherl 1957:387; Pedroso & Baptista 2004:150, 151, 153.

Type-localities.—BRAZIL: *São Paulo*: Cubatão, M. Lutz (Female holotype, FIOCRUZ, lost). Female neotype, herein designated: *São Paulo*: Cubatão. Gerard Bandet (F, IBSP 1910 N).

Diagnosis.—The short spermatheca and copulatory bulb of *Trechona rufa* are similar to *T. venosa*. The female of *T. rufa* has a short spermatheca with a lobulate spermathecal head (Fig. 4) and two rows of black setae dividing the scopula of tarsus III (Fig. 1). In *T. venosa*, the spermathecal head is rounded, without lobes, and the scopula of tarsus III is undivided, without setae. The male of *T. rufa* has a globular bulb, with a large distal membrane (Figs. 6–8). In contrast, the male of *T. venosa* has a piriform bulb, with a smaller distal membrane. Both sexes of *T. rufa* also have a lighter color pattern than *T. venosa*, with a predominance of brownish or reddish-brown hues. Also, *T. rufa* is smaller (body length 38.5–44.1, male 25.7–36.5) than *T. venosa* (body length 46.3–56.7, male 37–39.4). For *T. venosa* characters, see Pedroso & Baptista (2004).

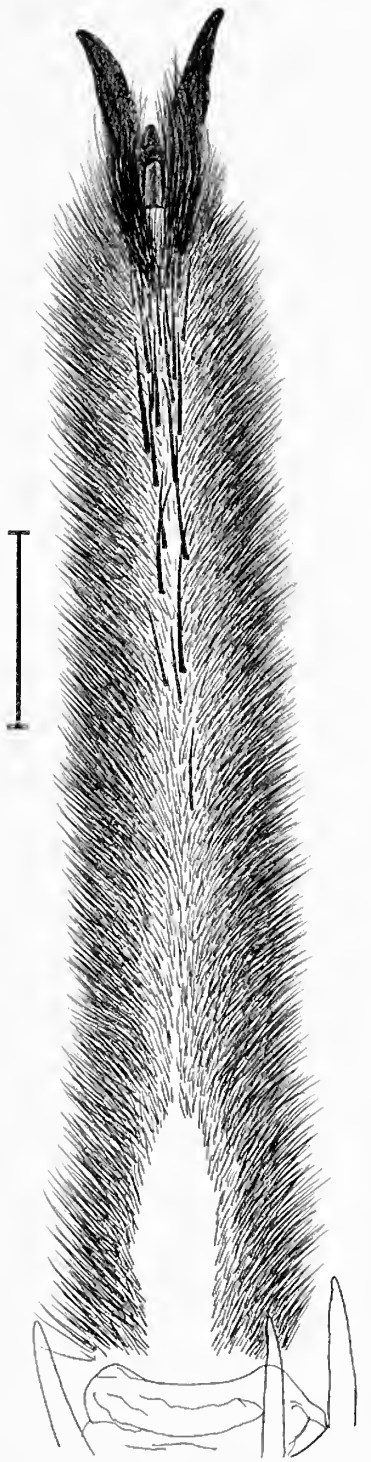

Figure 1.—Female (MNRJ 4175) from Atibaia, São Paulo state. Tarsus III, ventral view. Scale = 1 mm.

Description.—*Measurements.* Body total length. Females (n = 5): 40.3 (38.5–44.1). Males (n = 5): 31.7 (25.7–36.5). Carapace length. Females (n = 5): 16.1 (14.2–18.3). Males (n = 5): 13.6 (11.4–15.5). Leg I total length. Females (n = 5): 57.5 (54.0–61.8). Males (n = 5): 69.8 (65.0–75.5).

Female: Cephalothorax: dorsum brown or reddish-brown, with gray covering setae and some scattered black setae.

Figure 2.—Male (MNRJ 4179) from Ribeirão Grande, São Paulo state. Joint tibia-metatarsus I (left), ventral view. Scale = 1 mm.

Figure 3.—Male (MNRJ 4179) from Ribeirão Grande, São Paulo state. Joint tibia-metatarsus I (left), retrolateral view. Scale = 1 mm.

Clypeus with an average of eight erect setae, turned forward. Anterior portion of the eye tubercle with some small erect setae. Eye tubercle darker than the surrounding areas. Chelicerae black or dark reddish-brown, turning to black in direction of the distal portion. Sternum colored as the carapace, with gray covering setae and black erect setae scattered throughout the surface. Labium colored as the carapace, but its base is a bit darker. Without covering setae and with black setae thinner than the ones found at the sternum. Abdomen: dark brown, with six beige stripes, shaped as chevrons or a series of inverted "V" over the dorsum and sides. Setae black, erect, spread over the dorsum. Spinnerets with three equal-sized articles. Pedipalps: dark brown, with glabrous, shiny, longitudinal stripes. Coxa without spines. Ventral face covered by thin setae and black erect setae, which get thinner towards the reddish maxillary scopula. Anterior area with around 25 distinct cuspules. Dorsal face with setae covering the distal portion. Trochanter without spines. Dorsal face with setae covering the distal portion. Femur with one single lateral and two unpaired dorsal spines. Patella with a basal prolateral spine. Tibia bearing 10–13 spines, not arranged in rows, its ventral face with one basal, one medial, and two distal pairs. The remaining spines are placed on the prolateral and retrolateral sides. Tarsus with scopula and two spines on each side. Dorsal face with thin, covering, setae and several scattered, black, erect setae. Legs: color as in carapace, with glabrous, shiny, longitudinal stripes. Tarsi cracked (i.e., with cuticle presenting thin, membranous lines, separating the hard cuticle in pieces), especially on the ventral face, and with a row of trichobothria on the dorsal face. Tarsi I–IV with well marked scopula. Only metatarsi I–II with well marked scopula. Tarsi I–II with scopula interrupted by a small glabrous stripe and without black setae on the ventral side. Tarsi III–IV with scopula interrupted by a row of spiniform setae (Fig. 1). Leg I: coxa without spines. Ventral side with covering setae and black erect setae. Dorsal face with setae covering the distal portion. Trochanter as in pedipalp. Femur bearing four spines, from which three are dorsal and one, placed at the posterior portion, is prolateral. Patella without spines. Glabrous stripes wider than those found in femur and tibia. Tibia with one pair of ventral spines near the distal

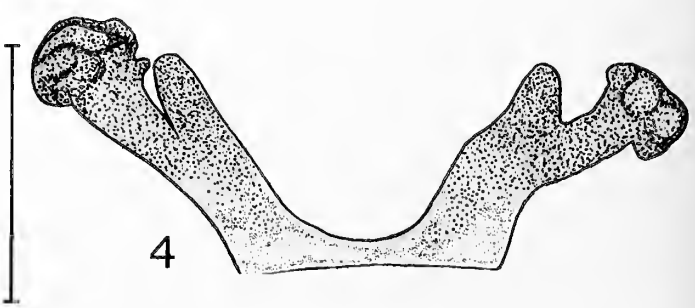

Figure 4.—Female (MNRJ 4175) from Atibaia, São Paulo state. Spermatheca, dorsal view. Scale = 1 mm.

Figure 5.—Male (MNRJ 4179) from Ribeirão Grande, São Paulo state. Pedipalp (left), terminal articles and bulb, retrolateral view. Scale = 1 mm.

Figure 6.—Male (MNRJ 4179) from Ribeirão Grande, São Paulo state. Bulb (left), retrolateral view. Scale = 1 mm.

margin and one or two unpaired spines at the basal portion. Prolateral face with one or two unpaired spines. Metatarsus bearing four or five spines on the ventral side, from which two to three unpaired ones are found on the basal portion and one pair near the distal margin. Dorsal side as in tarsus I. Tarsus without spines, with ventral scopula. Covering setae and several black erect setae spread at the dorsal side. Leg II: coxa, trochanter, and femur as in leg I. Patella with a prolateral spine at the distal portion. Tibia bearing 6–7 spines, not arranged in rows, from which one ventral pair is placed at the distal margin. Metatarsus with six spines, from which one dorsal pair is placed near the distal margin, three unpaired dorsal spines at the basal region, and one prolateral spine at the middle portion. Dorsal side as in tarsus. Tarsus as tarsus I. Leg III: coxa and troehanter as in leg I. Femur with 7–10 spines on the dorsal and lateral faces. Patella as in leg II. Tibia with 10 spines. One pair at the basal region, one pair at the middle and one pair at the distal margin of the ventral face, the remaining spines are two unpaired at the prolateral face and two unpaired at the retrolateral face. Metatarsus with 13–18 spines, from which 5 are always placed on the distal margin. Scopula not well-marked. Tarsus with a small row of black setae interrupting the distal portion of the scopula. Leg IV: coxa and trochanter as in leg I. Femur with 4 to 6 spines at the dorsal face. Patella without spines. Tibia with 9–12 spines, not arranged in rows. Metatarsus with 16–20 spines. Scopula almost unnoticeable. Tarsus with a middle longitudinal row of black setae interrupting the whole length of the scopula. Genitalia (Fig. 4): vulva composed of two spermathecae connected by a common membranous atrium. Spermathecae with a roundish head slightly flattened at the distal end and a subdistal anterior branch of size varying from almost the same length as the head branch to much smaller than it.

Male: Cephalothorax: carapace with somewhat darker color than females, but similar thin, covering setae and stouter setae. Clypeus with five erect setae, turned frontward. Eye tubercle as in females. Chelicerae as in females, but shorter and less robust. Inner margin with a row of thirteen to sixteen teeth. Sternum brown, a bit lighter than the carapace, smaller than in females, but longer than wide. Labium as in females, but with fewer setae. Abdomen: dark brown or black, with black erect setae spread over the dorsum. Stripes as in females. Spinnerets a little longer than in the females, with the last article longer than the others. Pedipalps: coxa as in females. Trochanter without spines and with a few black erect setae. Ventral face with a knob covered with several black erect setae. Femur with five to six spines, placed at the dorsal and lateral faces. Patella without spines. Tibia bearing 7–9 spines, not arranged in rows. Tarsus short, cylindrical, parted in two at the distal portion around the bulb insertion. Copulatory bulb described in the male genitalia below. Tarsi long and

Figure 7.—Male (MNRJ 4179) from Ribeirão Grande, São Paulo state. Bulb (left), frontal view. Scale = 1 mm.

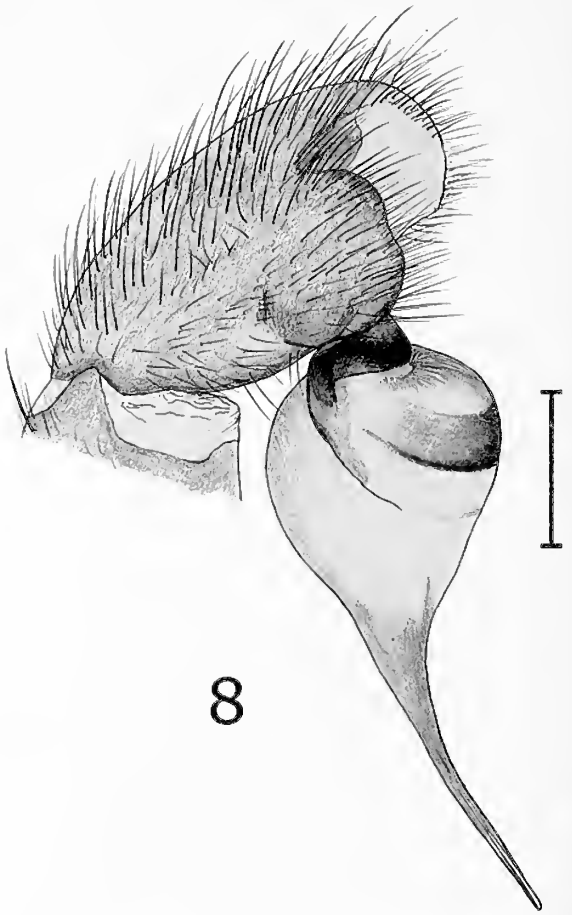

Figure 8.—Male (MNRJ 4179) from Ribeirão Grande, São Paulo state. Bulb (left), prolateral view. Scale = 1 mm.

distinctly cracked, with well-marked scopula. Dorsal face with black erect setae and few covering setae. A row of trichobothria placed between the spines over the length of the tarsi. Leg I: coxa and trochanter as in females. Femur with 7–11 spines, not arranged in rows, at the dorsal and lateral faces. Patella without spines or bearing one prolateral spine. Tibia with 6–9 spines, not arranged in rows. Distal margin with a large apophysis at the prolateral side (Figs. 2, 3). Metatarsus long and with scopula, bearing 5 spines, from which the ventral face has one at the distal margin and three at the basal and middle portions. Prolateral face with one spine. Basal portion displaying a shallow depression following a small knob bearing one spine (Figs. 2, 3). Leg II: coxa and trochanter as in leg I. Femur with 6–10 spines at the dorsal and lateral faces. Patella with one prolateral spine. Tibia as in leg I. Metatarsus long and with scopula, bearing 5–7 spines, not arranged in rows, from which one ventral pair is always found at the distal margin. Leg III: coxa and trochanter as in leg I. Femur with 10–12 spines at the dorsal and lateral faces. Patella as in leg II. Tibia bearing 8–11 spines, not arranged in rows, including one basal, one middle and one distal pair at the ventral side, and the remaining spines found in the lateral faces. Metatarsus long and with scopula, bearing 18–21 spines, not arranged in rows, from which 5 spines are always found at the distal margin. Leg IV: coxa and trochanter as in leg I. Femur with 9–12 spines at the dorsal and lateral faces. Patella without spines or bearing one prolateral spine. Tibia bearing 8–12 spines, not arranged in rows, from which one pair is always found at the distal margin. Metatarsus long and with scopula not well-marked, bearing 20–23 spines, not arranged in rows. Genitalia (Figs. 5–8): bulb almost piriform, with an "S"-shaped regular curve at its internal face (Figs. 5, 6), tapering regularly to a long, thin embolus, which bears a small whitish membranous area at its tip (Figs. 6–8).

Distribution.—Known only from the Atlantic Forest at São Paulo state, southeastern Brazil, spreading over a wide coastal area, from Ribeirão Grande to Ilhabela, and north up to Atibaia, at the southern slope of Mantiqueira mountain chain.

Material examined.—BRAZIL: *São Paulo*: no further locality (1 F, IBSP 3696); no further locality (1 F, IBSP 10804); no further locality, 14.IX.1965, inflicted bite in a patient of the Vital Brazil Hospital. (1 F, IBSP 1910 E); Barragem Passareuna (unknown locality). (1 F, IBSP 3569); Atibaia. XII.2002 (1 F, 1 young, MNRJ 04175); Atibaia. (1 young, IBSP 9754); Caraguatatuba, V-2007, S. Potsch et al., pitfall traps (2 M, MNRJ) Cubatão (1 M without palps, IBSP 1910); Cubatão. G. Bandet (2 F, IBSP 1910 N); Cubatão, Serra de Cubatão. VI.1972. G. Bandet (5 F, 1 young, IBSP 1910 Q); Diadema. 24.VII.1995. Tadeu (1 F, IBSP 10806); Diadema. 24.VII.1995. Tadeu (1 M, IBSP 10807); Diadema. 24.VII.1995. Tadeu (1 young, IBSP 10808); Diadema. 24.VII.1995. Tadeu (1 F, IBSP 10809); Diadema.

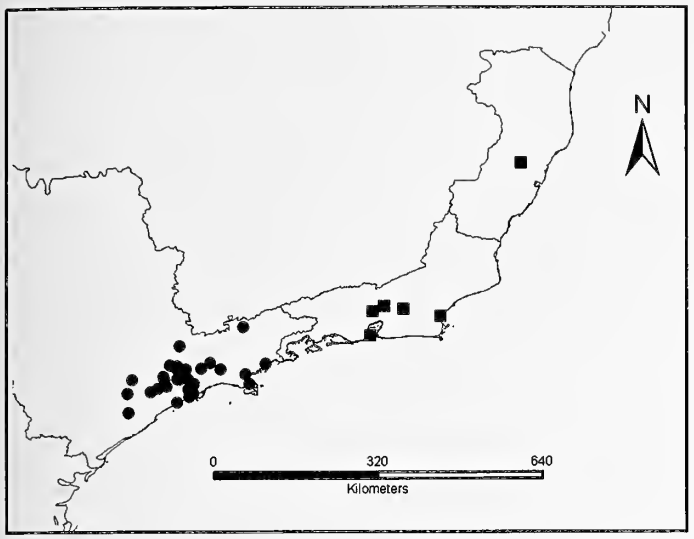

Figure 9.—Distribution of *Trechona rufa* (black circles) and *Trechona venosa* (black squares) in the states of Espírito Santo, Rio de Janeiro and São Paulo, Brazil.

24.VII.1995. Tadeu (1 F, IBSP 10811); Diadema. 30.VII.1995. R. Bertani & F. Palinger (1 F **Neotype**, IBSP 8027); Diadema. 30.VII.1995. R. Bertani et al. (1 F, IBSP 10791); Embu. 30.V.1989. D. Catunda (1 M, IBSP 10790); Embu-Guaçu. 6.XII.1999. A.A. Reis (1 M, IBSP 7964); Guararema. 20.VIII.1979. M. do C. Ruiz (1 M, IBSP 1910 L); Ilhabela, Ilha de São Sebastião. (1 F, IBSP 3666); Ilhabela, Ilha de São Sebastião. 1963. Urban (1 young, MZSP C3922); Itapecerica da Serra (1 M, IBSP 10805); Juquiazinho (may be Tapiraí, Juquiazinho trail or Peruíbe, Juquiazinho beach). (1 F, IBSP 1910 H (ex 4031)); Juquitiba. (1 F, IBSP 1910 D); Juquitiba. (1 F, IBSP 1910 K); Juquitiba. 07.XI.1983. H. Campos (1 young, IBSP 10797); Juquitiba. 18.VIII.1986. I. Biasi (1 M, IBSP 10794); Juquitiba. 26.V.1995. Prefeitura Municipal de Juquitiba (1 M, IBSP 10795); Mauá. 27.VIII.1998. E. Nechar (1 M, IBSP 10801); Miracatu. (1 F, IBSP 1910 F); Miracatu. 05.VI.2000. M. A. Yamasol (2 F, IBSP 8368); Mogi das Cruzes. (1 F, IBSP 3349); Mogi das Cruzes. VIII.1941. J. Meissner (1 F, MZSP 3154); Mogi das Cruzes. (1 M, IBSP 3801); Mongaguá. 16.IV.1961. (3 F, 1 young, IBSP 1910 O); Piedade. (1 F, IBSP 1910 G); Praia Grande. (1 young, IBSP 3383 B); Praia Grande. 17.VI.1949. J. Dotta (2 F, 1 M, 1 young, IBSP 1910 P); Raposo Tavares Highway, Km 31. (1 M, IBSP 3802); Ribeirão Grande, Sumidouro. 1–9.VI.2003. R. Bernils & Stender (1 M, MNRJ 04176); Ribeirão Pires. (1 F, IBSP 1910 B); Rio Grande da Serra. 5.II.1986. L. C. Genova (1 F, IBSP 10800); Salesópolis, Boracéia. 07.IX.1966. N. Papavero (1 M, MZSP 5656); Santo André, Alto da Serra. 18.III.1943. F. Lane & B. Soares (1 young, MZSP 26188); Santo André, Paranapiacaba. VI.1980. (1 F, IBSP 1910 I); Santo André, Paranapiacaba. (1 M, IBSP 3496); Santos, Serra de Santos, Meio da Serra. 09.IV.1956. Portugal & Tremoços (1 F, MZSP 1246); Santos-Jundiaí railway, Km 38. (1 M, IBSP 1910 J); São Bernardo do Campo. 06.IX.1996. Glasurit do Brasil (1 M, IBSP 10803); São Bernardo do Campo. 01.IV.1999. L.C. Aihara (1 F, IBSP 10799); São Lourenço da Serra. 12.IX.2001. A. Leme (1 M, IBSP 9188); São Paulo. (1 F, IBSP 3482); São Paulo. (1 F, IBSP 3591); São Paulo. 1920. E. Garbe (1 F, MZSP 325); São Paulo. 29.V.1998. O. Luiz (2 M, IBSP 8251); São Paulo, Caucaia. (1 young, IBSP 3530); São Paulo, Horto Florestal. (1 F, IBSP 2980); São Paulo, Horto Florestal. (1 M, IBSP 2974); São Paulo, Itaquera. 18.VI.1998. S. Lellis (1 M, IBSP 8249); São Paulo, near Guarapiranga dam. 29.VIII.2002. (1 F, IBSP 9865); São Paulo, Jaraguá. 20.V.1971. (1 M, IBSP 1910 M); São Paulo, Tucuruvi. 4.VII.1986. (1 M, IBSP 1910 C); Tapiraí. 6.V.2003. C.A. Falcetti (1 F, IBSP 10158).

Doubtful records.—The following records, representing juvenile specimens that could not be assigned to either *T. rufa* or *T. venosa*, are in the region between the ranges of the two species. BRAZIL: *São Paulo*: Ubatuba. 13.X.1985. R.L.C. Baptista (1 young, MNRJ 04174); Ubatuba, Praia Domingos Dias. 24.VI.1975. (1 young, IBSP 1910 A). *São Paulo?*: Serra da Bocaina. 01–31.VII.1961. M.A. Vulcano (1 young, MZSP 21689); Serra da Bocaina, Fazenda Bonito. 01–28.I.1963. M.A. Vulcano (1 young, MZSP 21689);

Comments.—Since the redescription of *Trechona venosa* (Pedroso & Baptista 2004), we examined many additional specimens of *T. rufa*, which allowed us to clearly separate it from the former species. Therefore, *T. rufa* is herein considered a valid species and removed from the synonymy of *T. venosa*.

Unfortunately, the dry, pinned holotype and the other specimens of *T. rufa* cited by Vellard (1924) were lost, as the arachnological collection of the Fundação Oswaldo Cruz (FIOCRUZ), Rio de Janeiro, was entirely destroyed, according to the former curator of Entomology, S. Oliveira (pers. comm.). Therefore, a neotype for *T. rufa*, collected at its type-locality, is herein designated.

The geographical boundary between *T. rufa* and *T. venosa* seems to fall somewhat along the coastal forests from eastern São Paulo and western Rio de Janeiro states (see Fig. 9). Recently, we examined two males of *T. rufa* from Caraguatatuba, which extends the species range far to the east. On the other hand, the westernmost record for *T. venosa* is Rio de Janeiro, Rio de Janeiro state. We were able to examine only immature specimens from intermediate localities, as Ubatuba, São Paulo state, and Paraty, Rio de Janeiro state, but it is not possible to make an accurate determination as they do not bear the characters used to diagnose *Trechona* species. Additional mature specimens from intermediate localities, as Angra dos Reis, Paraty or Ubatuba, would allow a more accurate determination of the distribution of both species.

Trechona adspersa Bertkau 1880

T. a. Bertkau 1880a:30.
T. a.: Bücherl 1957:386.

Trechona adspersa was based on a male holotype from Pedra-Açu, Teresópolis, Rio de Janeiro state, Brazil. The holotype should be deposited at the Institut Royal de Sciences Naturelles de Belgique (IRNSB). Most arachnids collected by the Belgian mission to Brazil and published in the same paper as *T. adspersa* were deposited in that museum., including 6 species of opilions (Kury 2003). Unfortunately, the holotype was not found in the IRNSB (L. Baert, pers. comm.) and is probably lost. The original deseription and illustration (pl. 1,

fig. 9) given by Bertkau (1880) shows a small spider (body length 11 mm), with many white spots arranged in transverse stripes and a male tarsus bearing an incrassate and short tibia and a copulatory bulb tapering regularly up to the tip of the embolus. Those characters strongly suggest some nemesiid species from southeastern Brazil. Additionally, a small female belonging to an undescribed nemesiid genus, collected in Teresópolis (MNRJ), agrees very well with the description of *T. adspersa*. Thus, *Trechona adspersa* Bertkau 1880 is herein considered a Nemesiidae ***incertae sedis***.

Trechona lycosiformis (C.L. Koch 1842)

Mygale l. C.L. Koch 1842:85
T. l.: C.L. Koch 1850:74.

Mygale lycosiformis was based on a female from Brazil and was subsequently transferred to the genus *Trechona* by C.L. Koch (1850). The holotype should probably be deposited at the Zoologische Sammlung, Museum für Naturkunde der Humboldt-Universität, Berlin (ZMHB), along with most material described by C.L. Koeh, or at the Zoologische Staatssammlung München (ZSMC), taking into account that the holotype belongs to the Perty collection. However, there is no mention of *Mygale lycosiformis* Koch 1842 (or *T. lycosiformis*) in the online catalog of the ZMHB arachnological collection (available at the SysTax site), although many other speeies deseribed by C.L. Koch in 1842 are deposited there. Also, after our request, the eurators of the Arachnida collection from ZMHB, Dr. Jason Dunlop, and from ZMSC, Dr. Roland Melzer, informed us that they were not able to locate any speeimen of *M. lycosiformis* in the respective collections (pers. comm.). Therefore, the holotype is considered lost. Based on the partial description and illustration (fig. 745) given by Koch (1842), this species is clearly not a *Trechona*. The uniformly brown color, without contrasting stripes on the abdomen, the hirsute body, the short spinnerets and the leg shape and proportion show that *Mygale lycosiformis* is a Theraphosidae *incertae sedis*. The preoccupied generic name *Mygale* Lamarck 1802 was replaced by *Avicnlaria* Lamarck 1818. However, it is evident that *M. lycosiformis* does not belong to *Avicularia* as shown by its brown eolor and legs covered by moderately short and relatively sparse setae. Unfortunately, as this species eannot be placed with any certainty in one of the numerous Theraphosidae genera, we therefore consider the name *Mygale lycosiformis* as *Avicularia lycosiformis* (C.L. Koch 1842) ***comb. nov.***, ***nomen dubium***. It will be added to the already extensive list of 29 ***nomina dubia*** in *Avicularia* (Platnick 2008).

Trechona rogenhoferi (Ausserer 1871)

Diplura r. Ausserer 1871:179.
Endiplura r.: Simon 1892:179.
Endiplura r.: Fischel 1927:67.
T. r.: Raven 1985a:75.

Raven (1985) examined the holotype of *T. rogenhoferi*, from Brazil (no further data), and pointed out that the specimen has the typical lyra of *Trechona*, but had not indicated if it was mature or not. However, the small body size (19 mm) and the spinnerets as long as the abdomen (Ausserer 1871), indicate that it is a young specimen. The male from Brazil identified as *T. rogenhoferi* by Simon, cited and well-illustrated by Raven (1985:figs. 24–30), is clearly a male of *T. venosa*, as shown by the pyriform bulb (fig. 25) and deeply notched metatarsi, with a large spiniform apophysis (fig. 26). However, there is no indication if it is really conspecific with the holotype of *T. rogenhoferi*. Hence, this species is herein considered as a *nomen dubium*, as there is no indication of a precise type locality and very young specimens are not identifiable to species level. It is noteworthy to point out that *T. rogenhoferi* may be a junior synonym of *T. venosa* (if collected in Rio de Janeiro state) or a senior synonym of *T. rufa* (if collected in São Paulo state).

Trechona sericata Karsch 1879

T. s. Karsch 1879:545.

Trechona sericata was based on a female holotype from Bogotá, Colombia (body 34 mm long). The holotype is a pinned, dry specimen, deposited at the Zoological Museum, Humboldt University, Berlin (ZMHB). We were able to examine a photograph of the holotype habitus, kindly sent by ZMHB curator, Dr. Jason Dunlop. According to the photo and the original description (Karsch 1879), the holotype has posterior lateral spinnerets 1.5 × longer than the body and no transverse stripes on the abdomen. Also, Karsch had not eited any clavate setae on the pedipalp coxa. All the typieal *Trechona* species have shorter spinnerets (up to 70% of the length of the abdomen), transverse stripes on the abdomen and a thick plate of clavate setae on the pedipalp coxa. So, *Trechona sericata* should be excluded from the genus. The elongated spinnerets and legs with flexible tarsi indicate that this species might belong to *Linothele* Karsch 1879, or to *Ischnothele* Ausserer 1875. *Linothele* is a common genus in Colombia, with some species bearing very long spinnerets and flexible tarsi. *Ischnothele* is also found in Colombia, represented by *Ischnothele caudata* Ausserer 1875, a widespread species and the only one known to occur in that country (Coyle 1995). Taking into consideration the elongated abdomen, the relatively long legs, the shape of the carapace and the wide eye region of the holotype, it is evident that *T. sericata* belongs to *Linothele*, resembling *L. megatheloides* Paz & Platnick 1977. So, *Trechona sericata* = *Linothele sericata* (Karsch, 1879) ***comb. nov.***

DISCUSSION

Taking in account the changes above, only three valid species (*T. venosa*, *T. rufa*, *T. uniformis* Mello-Leitão 1935) and a *nomen dubium* (*T. rogenhoferi*) remain in the genus. All the valid species are restricted to the Atlantic Forest of Brazil. The records of *T. venosa* (Latreille 1832) for Amazonia and British Guyana are clearly misidentifications, as pointed out by Pedroso & Baptista (2004). Also, we have not found any specimens of *Trechona* from outside the Atlantic Forest in the examined collections or during our field trips to other regions.

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Spiders in wheat fields and semi-desert in the Negev (Israel)

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Abstract. Intensively cultivated arable land and semi-desert are two dominant habitat types in the arid agroecosystem in the northwest Negev Desert (Israel). The present study compares activity-densities and species richness of spiders in these distinctive habitat types. Sixteen wheat fields and twelve locations in the semi-desert were sampled during the winter growing season of wheat. Semi-desert habitats had more spider species and higher spider activity-densities than irrigated wheat fields. The majority of spider families, namely Gnaphosidae, Thomisidae, Salticidae, Zodariidae, Philodromidae, Dysderidae, and Clubionidae had significantly higher activity-densities in the semi-desert compared to wheat. Only two families, the Linyphiidae that strongly dominated the arable spider community and Corinnidae had higher activity-densities in wheat than in semi-desert. Out of a total of 94 spider species, fourteen had significantly higher activity-densities in semi-desert than in wheat fields and eight species had significantly higher activity-densities in wheat fields than in semi-desert. Spider families and species that dominated the semi-desert communities also occurred in the wheat fields but at lower activity-densities. In conclusion, the semi-desert is a potential source of spider species and families that may immigrate into arable fields during winter. In particular, active hunting spiders may be sustained in crops through immigration from nearby semi-desert habitats.

Keywords: Araneae, biodiversity, desert agroecosystem, habitat preference

Spiders rapidly colonize new habitats, which makes them important natural enemies of pest arthropods in annual crops. Because arable land is an ephemeral habitat, spider populations in crops are frequently depleted (Thomas & Jepson 1997; Marc et al. 1999; Thorbek & Bilde 2004). Owing to their high mobility, spiders are among the first predators to recolonize crop fields after management practices (Öberg & Ekbom 2006). However, intensification of agriculture in the past decades has led to more uniform landscapes, larger fields of monocultures, loss of natural habitats, and an increase in chemical and physical disturbance of crop habitats. These factors have mostly negative effects on spider densities and species richness in arable land (Topping & Lövei 1997; Marc et al. 1999).

Most arthropods persist more readily in habitats with perennial, structurally rich vegetation and litter layer than in uniform crop fields with a bare soil surface. The availability of non-crop habitats in agricultural landscapes is therefore crucial for arthropods, including spiders (Luczak 1979; Schmidt & Tscharntke 2005a). Non-crop habitats act as refuges where animals can find hiding places from adverse conditions and build up higher population levels. With only a few exceptions, spiders that dominate Central European arable crops depend on perennial habitats for overwintering (Schmidt & Tscharntke 2005a). Woods, hedgerows, field margins, or fallows act as biodiversity reservoirs for animals and plants in agricultural landscapes because they are nearly undisturbed and temporally persistent (Bianchi et al. 2006). Indeed, previous studies showed that spider density and species richness are reduced in arable land compared to neighboring semi-natural habitats with perennial vegetation (Topping & Lövei 1997; Pfiffner & Luka 2000; Lemke & Poehling 2002; Clough et al. 2005; Schmidt & Tscharntke 2005a; Öberg 2007; Öberg et al. 2007).

Habitat relations of spiders are well studied in agroecosystems of temperate climates zones. In contrast, knowledge of spider communities in arid agroecosystems is still scarce (Gavish-Regev et al. 2008). Differences in habitat conditions between crops and other habitats are more pronounced in arid than in temperate agroecosystems. Here, we present a replicated comparison of spider communities in wheat fields and semi-desert habitats, the two dominant habitat types in the northwest Negev. We tested for differences in species richness and activity-densities of spider families and species. In the Negev Desert, the distribution of spiders across crops and natural habitats may differ from that found in temperate climate for a number of reasons. For example, differences in moisture and primary productivity between cropland and natural habitats are more pronounced in the arid Negev desert compared to most other climatic zones. Arable land in the northwest Negev is intensely managed with high inputs of fertilizers and irrigation. Owing to mild winters, two crops are usually grown within a year, doubling the disturbance events in arable land compared to the one-year crop cycles in temperate climates. The semi-desert on the other hand is characterized by a long dry season during which plant growth comes to a halt. Rains fall from November to March, inducing growth of annual vegetation. Locally adapted arthropods – herbivores and their predators alike – are most active in spring (March–April), following the winter rains (Levy 1985, 1998).

The highly productive wheat fields might attract herbivores that will attract predators, spiders included. However, spider immigration and population growth is counteracted by the high disturbance regime of arable land. Since semi-desert is the native habitat type, the majority of spider families and species should be adapted to it and therefore reach higher activity-densities in semi-desert than in arable land. The following hypotheses were tested:

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1. Spider activity-density is higher in semi-desert than in wheat fields.
2. Species richness is higher in semi-desert than in wheat fields.
3. The majority of families and species prefer semi-desert over wheat fields.

METHODS

Study sites.—Spiders were sampled in sixteen fields of winter wheat (*Triticum aestivum* L.) and at twelve locations in natural semi-arid habitat in the northwestern Negev Desert in Israel. The sampling sites were scattered over an area of 30 × 30 km in a region with intensive agriculture northwest of the city of Beer Sheva (31°14′N, 34°45′E). This area is dominated by large fields of mostly annual crops. Two crops are grown within a year. The summer crops typically consist of cotton (*Gossypium* ssp.), sunflowers (*Helianthus annuus*), melons (*Cucumis* ssp.) or peanuts (*Arachis hypogaea*). In the winter months, mostly potatoes (*Solanum tuberosum*) and winter wheat are grown. The wheat is sown in November but germination and growth is induced by rain, usually in late November. If it does not rain in due time, farmers irrigate the fields to trigger growth. Depending on the availability of water, some fields are not irrigated or irrigated only occasionally. The wheat is harvested either as green fodder in March or in May–June for the grain. Management of the sampled wheat fields varied but no insecticide spraying was applied during the entire sampling season. All but four wheat fields were irrigated. The soils of the fields consisted of loess with varying proportions of sand. Semi-desert habitat is composed of loess and sandy soils and is mainly found along dry river beds (wadis) or borders on open semi-desert which is used as military training area. Nature reserves are part of the study area in the southwest and the north. Semi-desert habitats are scattered with perennial shrubs and geophytes. In some wadis eucalyptus and acacia trees were planted in recent decades. Annual vegetation consists of grass and herbaceous species and appears after winter rains. At the first sampling in mid-December, the semi-desert was devoid of green vegetation, while wheat growth had been triggered by irrigation and on average, the wheat was 16 cm (± 2.3 SE) high. By the second sampling in the second half of January, rain had induced plant growth in the semi-desert. At the third sampling in the second half of February, vegetation cover was estimated in both habitat types. Vegetation in the semi-desert consisted of 65% (± 5.2 SE) cover of annual vegetation and 1.4% (± 0.5 SE) of perennial vegetation. The wheat in the sampled fields covered 83% (± 7.4 SE) of the surface and was 83 cm (± 5.5 SE) high. Most semi-desert habitats are grazed by Bedouin sheep and goats. The study sites were spatially interspersed to avoid climatic differences between natural and arable sampling sites and to cover the range of climatic conditions in the area (Fig. 1). Landscapes around the study sites varied from crop-dominated to semi-desert dominated. The influence of landscape composition on the spider assemblages will be dealt with elsewhere.

Sampling.—Spiders were sampled by pitfall traps in sixteen wheat fields and twelve sites in the semi-desert. Twenty traps per site were situated at least 50 m from the border of the habitat. They were arranged in four subsets consisting of four traps in a square of 2 m edge length and a fifth trap placed in the centre of the square. Subsets were about 12 m apart. The traps were 10 cm deep with an opening diameter of 9 cm. The traps were buried in the ground such that the rim was level with ground surface and contained 150 ml of 50% ethylene glycol with a drop of detergent as trapping liquid. The traps were opened three times for one week each during the growing season of the winter wheat. The first sampling was done in mid-December, the second in the second half of January and the third in the second half of February. Upon retrieval, spiders were transferred to 70% ethanol. All individuals were identified to family and adult individuals to species or morphospecies (Levy 1985, 1998; Roberts 1995; Dippenaar-Schoeman & Jocque 1997; Proszynski 2003). The nomenclature followed Platnick (2008). Voucher specimens are deposited in the Arachnid Collection at Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev and in the National Collection of Arachnids at the Hebrew University of Jerusalem, Israel.

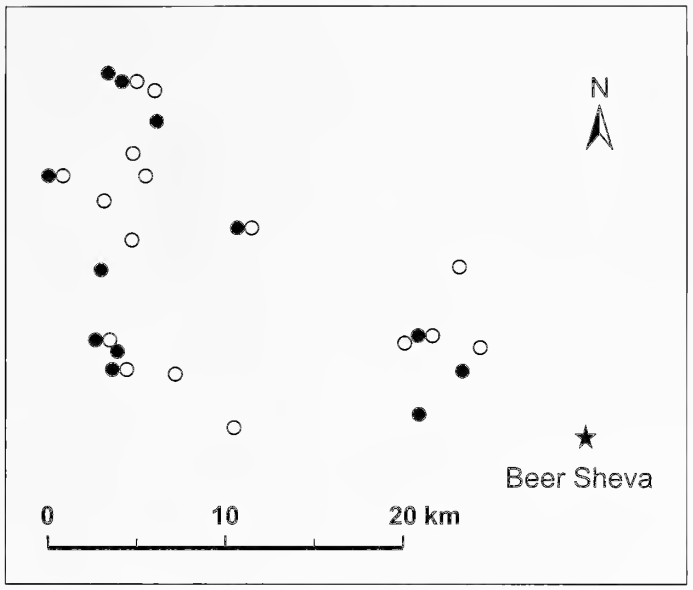

Figure 1.—Distribution of sampling sites in the northwest Negev. Open circles symbolize sampling sites in wheat fields and filled circles symbolize samplings sites in semi-desert.

Analyses.—The captures from the twenty traps and three sampling sessions were summed up for each site. Species richness, overall spider activity-densities and activity-densities per family were compared between the two habitat types using exact significance levels from Mann-Whitney U tests because assumptions for parametric tests were not always met (SPSS Inc. 2005). On the species level, the overall difference in spider communities between wheat fields and semi-desert was assessed with a multivariate redundancy analysis (RDA) and Monte-Carlo permutation test using the program CANOCO (ter Braak & Smilauer 2002). As the overall difference in spider communities between the two habitats was significant, habitat preference of each species could be tested with exact Mann-Whitney U tests using species-wise error rates (Moran 2003). Standard errors are given in text, tables and figures.

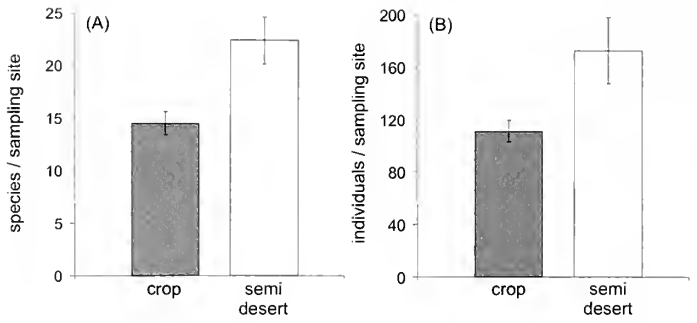

Figure 2.—(A) Species richness and (B) spider activity-density per sampling site in wheat fields versus semi-desert.

RESULTS

In total, 4093 spiders belonging to 26 families and 94 species were caught. Species richness was 54% higher in the semi-desert than in the wheat fields (exact Mann-Whitney U tests; $Z_{1,27} = -2.4$, $P = 0.013$; Fig. 2A). Spider activity-density showed a very similar pattern, and was 55% higher in the semi-desert than in wheat fields ($Z_{1,27} = -1.9$, $P = 0.058$, Fig. 2B). Of the thirteen most common families, only Linyphiidae ($Z_{1,27} = -3.3$, $P < 0.001$; Fig. 3) and Corinnidae ($Z_{1,27} = -2.0$, $P = 0.04$) showed significantly higher numbers in wheat fields. In contrast, eight families reached significantly higher activity-densities in the semi-desert than in crops. In the order of their overall activity-density, these were ground spiders (Gnaphosidae) $Z_{1,27} = -3.3$, $P = 0.001$, crab spiders (Thomisidae) $Z_{1,27} = -3.7$, $P < 0.001$, jumping spiders (Salticidae) $Z_{1,27} = -2.2$, $P = 0.024$, ant spiders (Zodariidae) $Z_{1,27} = -4.4$, $P < 0.001$, running crab spiders (Philodromidae) $Z_{1,27} = -3.2$, $P = 0.001$, woodlouse spiders (Dysderidae) $Z_{1,27} = -3.9$, $P < 0.001$, running foliage spiders (Liocranidae) $Z_{1,27} = -2.4$, $P = 0.01$ and sac spiders (Clubionidae) $Z_{1,27} = -3.5$, $P < 0.001$. Wolf spiders (Lycosidae), cobweb spiders (Theridiidae), and giant crab spiders (Sparassidae) showed no significant habitat preference. On the species level, spider communities differed significantly between wheat fields and semi-desert (RDA; $F_{1,27} = 7.5$, p = 0.0001). The difference accounted for 22.4% of all variation in community composition. Out of the 94 species found, eight species had significantly higher activity-densities in wheat fields than in semi-desert (Table 1). Six of them were sheetweb spiders, including the overall most common *Alioranus pastoralis* and the exotic North American species *Mermessus denticulatus*. Fourteen species from six families had significantly higher activity-densities in semi-desert than in wheat fields (Table 1).

DISCUSSION

In the northwest Negev, spider activity-density and species richness were higher in the semi-desert than in winter wheat. Ground spiders (Gnaphosidae), a species rich family in Israel, contributed most to the overall activity-density in the semi-desert. In addition, crab spiders (Thomisidae) and ant spiders (Zodariidae) reached high activity-densities in the semi-desert. Despite the preference of most families for the semi-desert, they also occurred in wheat fields at low activity-densities (Fig. 3). Probably, immigration from semi-desert into wheat fields is

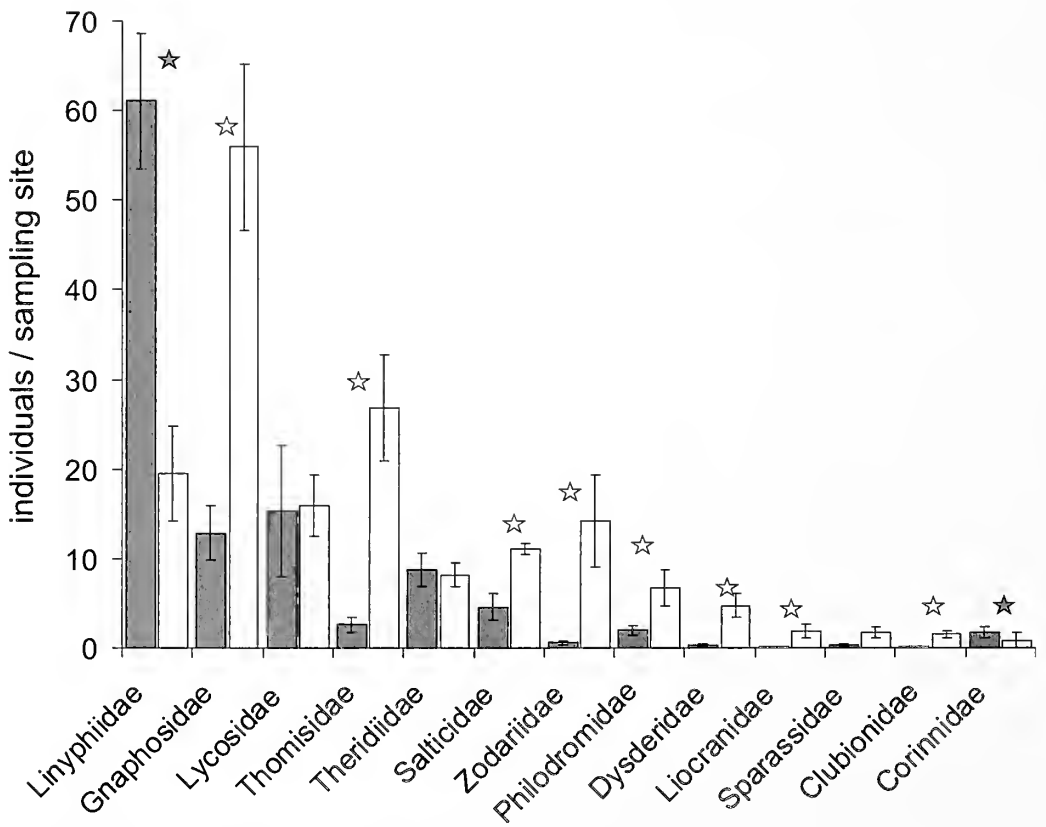

Figure 3.—Activity-densities per sampling site of spider families in wheat fields (grey) versus semi-desert (white). Filled stars represent a significant preference for the crop; open stars represent significant preference for semi-desert.

Table 1.—Average activity-densities (± SE) of spider species in the $n = 16$ wheat fields and $n = 12$ semi-desert locations, corresponding to 420 trap-days per location. Activity-densities that are significantly higher in one of the habitat types are given in bold. Z and P are according to exact Mann-Whitney U tests. Species with less than ten individuals (number of individuals in wheat fields versus semi-desert in parentheses): Agelenidae: *Lycosoides coarctata* (Dufour 1831) (1,0), Araneidae: *Hypsosinga albovittata* (Westring 1851) (0,1), Clubionidae: *Clubiona genevensis* L. Koch 1866 (0,5), Dictynidae: *Lathys* sp11 (0,2), Dysderidae: *Dysdera* sp12 (1,5), *Tedia abdominalis* Deeleman-Reinhold 1988 (1,8), *Tedia oxygnatha* Simon 1882 (2,2), Filistatidae: sp13 (0,1), Gnaphosidae: *Anagraphis pallens* Simon 1893(1,0), *Drassodes lutescens* (C.L. Koch 1839) (1,3), *Haplodrassus dalmatensis* (L. Koch 1866) (5,4), *Odontodrassus mundulus* (O. Pickard-Cambridge 1872) (0,7), *Pterotricha conspersa* (O. Pickard-Cambridge 1872) (0,1), *Talanites* sp14 (0,2), *Trachyzelotes* cf *jaxartensis* (Kroneberg 1875) (0,1), Linyphiidae: *Diplocephalus* cf *protuberans* (O. Pickard-Cambridge 1875) (4,0), *Lepthyphantes* sp15 (3,1), *Lepthyphantes* sp16 (5,4), *Pelecopsis* sp17 (1,0), *Sintula* sp18 (3,1), *Thaumatoncus* sp19. (0,3), *Thaumatancus* sp20 (1,1), sp21 (1,6), sp22 (0,1), sp23 (1,0), Liocranidae: *Mesiotelus* sp24 (0,5), Lycosidae: sp25 (1,0), *Trochosa* sp26 (2,1), Nemesiidae: *Nemesia* sp27 (0,1), Philodromidae: *Thanatus meronensis* Levy 1977 (0,1), sp28 (1,0), Prodidomidae: sp29 (1,0), Salticidae: *Aelurillus conveniens* (O. Pickard-Cambridge 1872) (0,1), *Aelurillus politiventris* (O. Pickard-Cambridge 1872) (0,1), *Pellenes sinoni* L. Koch 1882 (1,7), *Salticus olivaceus* (L. Koch 1867) (0,1), *Salticus propinquus* Lucas 1846 (0,6), Sicariidae: *Loxosceles* sp30 (0,1), Theridiidae: *Enoplognatha deserta* Levy & Amitai 1981 (1,1), *Euryopis episinoides* (Walckenaer 1847) (0,1), *Latrodectus tredecimguttatus* (Rossi 1790) (0,1), *Steatoda erigoniformis* (O. Pickard-Cambridge 1872) (1,0), *Steatoda latifasciata* (Simon 1873) (4,0), *Steatoda manra* (Simon 1909) (1,0), *Steatoda triangulosa* (Walckenaer 1802) (1,0), *Theridion nigropunctatum* Lucas 1846 (0,1), Thomisidae: *Ozyptila judaea* Levy 1975 (0,4), *Ozyptila omega* Levy 1975 (0,2), *Xysticus caperatus* Simon 1875 (1,0), *Xysticus edax* (O. Pickard-Cambridge 1872) (1,7), *Xysticus kempeleni* Thorell 1872 (0,1), *Xysticus pomiscuus* O. Pickard-Cambridge 1876 (0,1), Zodariidae: *Zodarion lutipes* (O. Pickard-Cambridge 1872) (0,1), Zoropsidae: *Zoropsis lutea* (Thorell 1875) (0,2).

Family	Species	Wheat fields	Semi-desert	Z	P
Corinnidae	*Phrurolithus* sp1	**1.75 ± 0.65**	0.00 ± 0.00	−2.8	0.007
	Corininae sp2	0.00 ± 0.00	0.83 ± 0.83	−1.2	0.429
Dictynidae	sp3	0.00 ± 0.00	0.83 ± 0.75	−1.7	0.175
Dysderidae	*Dysdera westringi* O. Pickard-Cambridge 1872	0.13 ± 0.09	**1.58 ± 0.29**	−3.9	0.000
	Harpactea sp4	0.00 ± 0.00	**1.83 ± 0.91**	−2.4	0.024
Gnaphosidae	*Haplodrassus mediterraneus* Levy 2004	0.56 ± 0.22	1.50 ± 0.61	−1.3	0.219
	Haplodrassus morosus (O. Pickard-Cambridge 1872)	0.31 ± 0.18	1.67 ± 0.80	−1.2	0.204
	Micaria corvina Simon 1878	0.25 ± 0.19	**14.42 ± 5.60**	−3.2	0.001
	Micaria ignea (O. Pickard-Cambridge 1872)	0.06 ± 0.06	0.92 ± 0.50	−1.9	0.101
	Micaria pallipes (Lucas 1846)	0.00 ± 0.00	**1.58 ± 0.73**	−2.8	0.008
	Minosia spinosissima (Simon 1878)	1.06 ± 0.87	**3.83 ± 0.90**	−3.1	0.001
Linyphiidae	*Alioranus pastoralis* (O. Pickard-Cambridge 1872)	**21.50 ± 3.37**	7.17 ± 2.04	−3.0	0.002
	Bathyphantes cf *extricates* (O. Pickard-Cambridge 1876)	**0.75 ± 0.28**	0.00 ± 0.00	−2.6	0.017
	Erigone dentipalpis (Wider 1834)	**0.69 ± 0.22**	0.00 ± 0.00	−2.6	0.016
	Gongylidiellum sp5	**16.56 ± 5.12**	0.08 ± 0.08	−3.3	0.001
	Mecopisthes monticola Bosmans 1993	1.56 ± 1.38	5.67 ± 3.72	−0.9	0.463
	Meioneta psendornrestris (Wunderlich 1980)	0.75 ± 0.27	0.75 ± 0.28	−0.2	0.901
	Mermessus denticulatus (Banks 1898)	**6.81 ± 2.48**	0.08 ± 0.08	−3.2	0.001
	Pelecopsis cf *inedita* (O. Pickard-Cambridge 1875)	0.44 ± 0.32	0.75 ± 0.75	−0.6	0.613
	Pelecopsis sp6	0.69 ± 0.24	0.67 ± 0.43	−0.8	0.467
	Trichoncoides piscator (Simon 1884)	**8.13 ± 2.07**	0.08 ± 0.08	−3.5	0.000
	sp7	0.25 ± 0.17	**2.67 ± 1.05**	−2.3	0.013
Liocranidae	*Liocranum* sp8	0.06 ± 0.06	0.92 ± 0.45	−1.9	0.085
Lycosidae	*Alopecosa* cf *albofasciata* (Brullé 1832)	0.06 ± 0.06	**1.00 ± 0.44**	−2.3	0.041
	Pardosa cf *proxima* (C.L. Koch 1847)	**9.50 ± 5.88**	0.17 ± 0.17	−2.9	0.004
	sp9	1.00 ± 0.52	**6.67 ± 2.04**	−3.4	0.000
Philodromidae	*Thanatus vulgaris* Simon 1870	0.06 ± 0.06	1.00 ± 0.59	−1.9	0.085
Salticidae	*Aelurillus* cf *aeruginosus* (Simon 1871)	3.56 ± 1.18	5.58 ± 1.76	−0.9	0.394
Sparassidae	*Micrommata formosa* Pavesi 1878	0.19 ± 0.10	1.42 ± 0.60	−1.9	0.057
Theridiidae	*Enoplognatha gemina* Bosmans & Van Keer 1999	3.50 ± 0.92	3.50 ± 1.06	−0.19	0.863
	Enoplognatha macrochelis Levy & Amitai 1981	1.38 ± 0.50	0.75 ± 0.25	−0.2	0.887
	Steatoda albomaculata (De Geer 1778)	1.31 ± 0.99	0.00 ± 0.00	−2.1	0.053
	Steatoda paykulliana (Walckenaer 1805)	0.25 ± 0.11	0.67 ± 0.43	−0.2	0.710
Thomisidae	*Ozyptila patellibidens* Levy 1999	0.44 ± 0.18	**5.58 ± 1.60**	−2.9	0.003
	Ozyptila sp10	1.31 ± 0.69	12.92 ± 6.37	−0.8	0.452
	Ozyptila tricoloripes Strand 1913	0.25 ± 0.17	0.75 ± 0.25	−1.9	0.061
	Xysticus bliteus (Simon 1875)	0.31 ± 0.18	**2.17 ± 0.91**	−2.4	0.019

Table 1.—Continued.

Family	Species	Wheat fields	Semi-desert	Z	P
	Xysticus cristatus (Clerck 1757)	0.00 ± 0.00	**1.83 ± 0.95**	−2.8	0.008
	Xysticus xerodermus Strand 1913	0.00 ± 0.00	**1.75 ± 0.65**	−3.4	0.001
Zodariidae	*Lachesana rufiventris* (Simon 1873)	0.13 ± 0.13	0.75 ± 0.45	−1.4	0.242
	Ranops expers (O. Pickard-Cambridge 1876)	0.00 ± 0.00	**5.83 ± 2.64**	−2.8	0.008
	Zodarion nitidum (Audouin 1826)	0.00 ± 0.00	**2.42 ± 1.57**	−2.8	0.008

responsible for the presence of these desert-preferring spiders. Semi-desert, therefore, serves as a source for spider migration into the arable fields and thus contributes to a more diverse spider fauna in wheat fields in this desert agroecosystem (Gavish-Regev 2008). Despite the presence of some desert spiders, the wheat fields were dominated by one family. More than half of the individuals in wheat fields belonged to the sheetweb spiders (Linyphiidae), which showed a strong preference for this habitat. While sheetweb spiders dominate arable land both in Israel and in the temperate zone, the patterns in natural habitats are different. European natural habitats harbor more sheetweb spiders than arable land and act as sources for immigration of these spiders into fields (Schmidt & Tscharntke 2005a). This is not the case in the Negev where it is more likely that wheat fields act as a source for sheetweb spiders to spill over into the semi-desert (Tscharntke et al. 2005; Rand & Louda 2006; Rand et al. 2006).

The disturbance regime in arable land in the northern Negev is even higher than in Europe because two crops are grown per year. This means that operations such as harvest and tillage occur twice instead of once per year. Only very few families may be able to cope with this degree of disturbance. Sheetweb spiders show traits of typical pioneers and just as in temperate climate zones (Samu & Szinetar 2002; Nyffeler & Sunderland 2003; Schmidt & Tscharntke 2005a), they were also dominant in disturbed arable land sampled in the present study. However, the mechanism responsible for this dominance in the Negev fields may be different from temperate climate zones. Gavish-Regev et al. (2008) found similar numbers of sheetweb spiders in open traps and in closed emergence traps that were installed after crop sowing, which suggests that sheetweb spiders do not immigrate, but are residents in crop fields in the Negev Desert. Just like other arthropods, sheetweb spiders are negatively affected by mechanical management practices in the crops, but they apparently rebuild populations from egg sacs or individuals that survived sowing. This is a different mechanism than in temperate climate zones, where immigration by ballooning appears to result in the high dominance of sheetweb spiders in arable land (Nyffeler & Sunderland 2003; Schmidt & Tscharntke 2005b).

Spiders are sensitive to habitat structure (Marc et al. 1999; Bell et al. 2001). During the crop season, the ground of wheat fields is bare with hardly any litter. While sheetweb spiders can cope with the lack of litter, other ground dwellers avoid such habitats. Together with the high disturbance regime this can explain the low activity-densities in ground spiders (Gnaphosidae), crab spiders (Thomisidae) and sac spiders (Clubionidae) in wheat fields. Vegetation structure and litter layer determine microclimatic conditions that are important for spiders (Bell et al. 2001). Low humidity is one of the main factors limiting spider survival (Almquist 1971; Cardoso et al. 2007). Spiders avoid desiccation by seeking taller vegetation where humidity is higher (De Keer et al. 1989). The risk of desiccation is accentuated in arid environments and probably even more so for small species such as sheetweb spiders, which preferred the more humid and densely vegetated wheat fields over semi-desert. Except for the exotic *M. denticulatus*, little is known about the origin of sheetweb spider species in the agricultural land of the Negev. Sheetweb spiders are mostly a sub-arctic group, adapted to moderate temperatures and high humidity (Nyffeler & Sunderland 2003). Sheetweb spiders that occurred in the Negev before the development of agriculture were probably concentrated to a few relatively humid habitats. This pre-adaptation may now allow them to dominate arable land in the Negev desert. As an exception, one species of sheetweb spiders (morphospecies sp7) preferred semi-desert over wheat fields. In contrast to the majority of sheetweb spiders, active hunting spiders predominate in warmer regions because their foraging strategy is more efficient at warmer temperatures (Nyffeler & Sunderland 2003). Shady, slightly cooler habitat conditions might therefore have contributed to the low numbers of active hunting spiders in wheat fields.

Spider density is often determined by prey availability (Harwood et al. 2001). The intensive cultivation methods with irrigation and use of fertilizers lead to a high primary production in the studied wheat fields. This potentially attracts herbivores, which could in turn lead to higher prey abundance for spiders. Crop fields in the semi-desert might also, therefore, be an attractive habitat for desert spiders. Although spiders are generalist predators, some families have evolved prey preferences. The dominant Salticidae species in the present study is *Aelurillus aeruginosus* (Simon 1871), a predator of ants (Hymenoptera: Formicidae) (Li et al. 1999). *Aelurillus aeruginosus* reached higher activity-densities in the natural habitat. This corresponds to the habitat preference of their prey, because ants are usually scarce on ploughed soil (Dauber et al. 2005). Low activity-densities of ants in crop fields are likely to also explain the preference of ant spiders (Zodariidae) for the natural habitat, because this family also feeds predominately on ants. Small spiders in general and sheetweb spiders in particular feed mainly on soft bodied, small sized springtails (Collembola) (Sanders & Platner 2007). These arthropods are rare on dry soils and thus food for sheetweb spiders is scarce in semi-deserts (Nyffeler & Sunderland 2003). Finally, the semi-desert is the prevailing habitat type of the arid climate zone to which Negev spiders are adapted. One means of adaptation may be strongly seasonal activity patterns (Jiménez & Lobo 2006; Langlands et al. 2006; Cardoso et al. 2007).

In conclusion, spider diversity is concentrated in natural habitats not only in temperate climates but also in the semi-desert agroecosystem of the Negev. With respect to spider activity-density, a strong preference of sheetweb spiders for arable fields contrasted with the preference of the remaining spider families for the semi-desert. Accordingly, especially wandering spiders in desert crops are expected to benefit from the conservation of semi-desert in the agricultural landscape.

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Microhabitat use by *Peucetia flava* (Oxyopidae) on the glandular plant *Rhyncanthera dichotoma* (Melastomataceae)

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Abstract. Several studies have reported that plant structural components can exert strong influences on the density and distribution of spiders. However, little is known about which plant traits mediate specific associations between spiders and plants. In southeastern Brazil, the lynx spider *Peucetia flava* Keyserling 1877 (Oxyopidae) is commonly found on the plant *Rhyncanthera dichotoma* (Melastomataceae), a shrub that bears glandular trichomes. In this study we investigated if *Peucetia* occurs strictly on *Rhyncanthera* and what plant parameters influence the spiders' distribution. In addition, we recorded the vertical distribution of spiders of different ages in the plant canopy. Throughout the year *Peucetia* was observed only on the glandular plant *Rhyncanthera*, indicating that this association is specific and predictable. Statistical analysis showed no difference in the number of spiders between plants of *Rhyncanthera* with and without flowers, suggesting that this specific association is mediated by the presence of glandular trichomes, and not by reproductive structures. The distribution of *Peucetia* over the year was related to the number of arthropods on plants, as well as the number of leaves and height of the host plants, indicating that *Peucetia* probably choose sites of high food availability. Adults and subadults occurred on higher places on the crown than young and juveniles.

Keywords: Plant architecture, glandular trichomes, spider-plant interactions

Spiders are among the most abundant and diverse arthropods on vegetation (Wise 1993; Foelix 1996; Romero & Vasconcellos-Neto 2006) and are strongly influenced by variations in plant architecture (Greenquist & Rovner 1976; Riechert & Gillespie 1986; Gunnarsson 1990, 1992, 1996; Romero & Vasconcellos-Neto 2005a). Moreover, spiders are recognized by their ability to choose microhabitats of better quality, i.e., they generally prefer those with high abundance of prey (e.g., reproductive branches) (Morse & Fritz 1982; Ward & Lubin 1993; Morse 2007). Yet, some spiders may choose substrata based on leaf morphology (e.g., Thomisidae, *Diaea*, Evans 1997). Although these studies reported spider selection for microhabitats, most of them refer to only a few taxonomic groups (e.g., Thomisidae, Salticidae, and Araneidae) (Romero & Vasconcellos-Neto 2006) and few studies describe how plant parameters influence the density of hunting spiders (e.g., Romero & Vasconcellos-Neto 2005a).

Recent studies have reported specific associations of spiders with specific plant features (Figueira & Vasconcellos-Neto 1991, 1993; Arango et al. 2000; Rossa-Feres et al. 2000; Romero 2001; Romero & Vasconcellos-Neto 2003, 2004a, b, c, 2005a, b, c; Dias & Brescovit 2004). To date, the better studied examples of botanical structures that mediate spider-plant interactions are architecture in rosettes and glandular trichomes (Romero 2006; Vasconcellos-Neto et al. 2007). While the former facilitates the encounter of prey and mates and can be used as sites for egg-laying and shelter for adults and immatures, the later trap insects that can be used as prey by some spiders (Romero & Vasconcellos-Neto 2003, 2004a, 2005a; Vasconcellos-Neto et al. 2007).

Up to ten species of the genus *Peucetia*, including two South American species, *P. flava* Keyserling 1877 and *P. rubrolineata* Keyserling 1877 (Oxyopidae), live strictly associated with many species of glandular plants in Neotropical, Neartic, Afrotropical, and Palearctic regions (Vasconcellos-Neto et al. 2007). However, few studies have investigated patterns of host plant use in *Peucetia*, especially which plant traits besides presence of glandular trichomes influence the distribution of spiders of this genus on their host plants (e.g., Louda 1982; Arango et al. 2000). In southeastern Brazil specimens of *P. flava* were reported to occur frequently on *Rhyncanthera dichotoma* (Nees) C.B. Clarke (Melastomataceae), a glandular shrubby plant that typically inhabits swamps (J.C. Morais-Filho & G.Q. Romero, pers. obs.). To better understand this system, the purpose of our study was to evaluate (1) if *Peucetia flava* occurs strictly on *Rhyncanthera* or randomly on any other plant species; (2) which plant parameters influence the distribution of this spider population; and (3) if there is some variation in the vertical distribution of *Peucetia* of different ages in the canopy of *Rhyncanthera*.

METHODS

Study area and organisms.—This work was done in a swamp along an affluent margin of a lake (elev. 494 m; 20°49′S, 49°20′W) in São José do Rio Preto city, northwest of São Paulo state, southeastern Brazil. The climate in this region is of the type Cwa-Aw of Köppen, characterized by a hot/rainy season in the summer and dry in the winter. The annual precipitation varies from 1100 to 1250 mm, receiving 85% of the rainfall in the rainy season (September–March) and only 15% in the cold/dry season (Barcha & Arid 1971).

Rhyncanthera dichotoma is a hydrophitic phanerogamic shrub (0.5–2.0 m high) that occurs in temporary aquatic ecosystems, and the flowering period of this plant occurs once a year between March and May. This plant is frequently inhabited by arthropods of various guilds, including

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phytophages (e.g., Curculionidae, Miridae, Aphididae, Homoptera) and predators (e.g., spiders, Reduviidae). Many insects (e.g., ants, Chironomidae, Aphididae) adhere to the glandular trichomes, which are very dense on leaves and young stems of this plant species. The spider *Peucetia flava* is the most common predator on this plant and uses it as foraging and reproductive site (J.C. Morais-Filho & G.Q. Romero, pers. obs.).

Voucher specimens of the spiders collected (males and females) were deposited in the Arachnological Collection of the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

Fidelity of *Peucetia* for host plant.—Data were obtained in June 2007 in an area of 800 m^2 (two independent plots: 10 × 30 m and 10 × 50 m). We inspected leaves and recorded the presence or absence of *P. flava* on stems of 90 individuals of *Rhyncanthera* and another 250 plants without glandular trichomes, those belonging to diverse families (e.g., Asteraceae, Melastomataceae, Poaceae, Zingiberaceae).

Plant parameters and distribution of *Peucetia*.—To verify if *P. flava* is more abundant on plants with flowers than without flowers, in March–April 2006 and April 2008 (the flowering periods) we counted the number of spiders on 8–22 individuals of *Rhyncanthera* with flowers and on 14–27 individuals without flowers. For each plant we also counted the number of leaves. Data were log (n + 1) transformed to equalize variances and then compared using ANCOVA, with presence or absence of flowers (treatment) as a fixed effect (two levels), years (2006 and 2008) as a fixed effect (two levels), and number of leaves as the covariate.

To verify what plant parameters influence *P. flava* distribution, we surveyed 16–32 plants monthly between December 2005 and December 2006. Data on plant height, number of leaves and flowers, and total number of arthropods (potential free prey and potential prey stuck to glandular triehomes) were assessed for each plant surveyed. We also recorded the number of *P. flava* of various ages. To test which plant parameters influence the distribution of spiders in each month over the year, we used multiple linear regressions (Zar 1996) with the total number of individuals of *Peucetia* as the dependent variable and the parameters plant height, number of leaves, flowers, and total number of arthropods as the independent variables. The multiple linear regression test concerning all these four independent variables detected multicollinearity. We then removed some independent variables following procedures suggested by Zar (1996): we first ran a linear regression analysis between all these independent variables and selected those with the smallest value of r^2 (i.e., height, number of leaves, and total number of arthropods). By this selection we excluded the independent variable "abundance of flowers" that was strongly related to the other independent variables because *R. dichotoma* produce flowers only once, in a short period of the year.

Vertical distribution among age classes.—To test if there is variation in the vertical distribution of *Peucetia* from different ages in the canopy of *Rhyncanthera*, we measured the body size of each spider and its proportional height in the crown of the plant. For this, we divided the height that the spider occupied in the crown by the height of the crown. We defined the height of the crown as the length between the highest tip of the plant and the base of the crown (i.e., the junction of the first secondary branch with the main trunk); thus, a value close to zero means that the spider is at the base of the crown, and value close to one indicates that the spider is at the tip of the plant. To categorize the instars the spiders were classified as young [total body length (cephalothorax + abdomen) ≤ 3.0 mm], juveniles (> 3.0 mm but ≤ 6.0 mm), subadults (females > 6.0 mm but < 9.0 mm; males > 6.0 mm but ≤ 7.0 mm, with a dilated palp and slightly orange abdomen) and adults (females ≥ 9.0 mm; males > 7.0 mm, with a dilated sclerotized palp and orange abdomen). Data on distribution of spiders of each age class were compared for each sampling period using ANOVA (Zar 1996). Prior to the analyses these proportions were arc-sin square root transformed for data normalizations. If necessary, we performed paired comparisons using Fisher's LSD *post hoc* test. The test was run only in December 2005 because in this period the power of the performed test was high (95%); in the remaining months the power of the performed test was very low, varying from 5-35%.

RESULTS

Fidelity of *Peucetia* for host plant.—Although we have observed several spider species on plants that do not bear glandular hairs, *Peucetia flava* was observed only on the glandular plant *Rhyncanthera dichotoma*. In June (2007), we found 44 individuals of *P. flava* on *Rhyncanthera dichotoma* and none on the other plant species without glandular hairs.

Plant parameters and distribution of *Peucetia*.—There was no statistical difference in number of spiders between plants with and without flowers, and this was the case both in 2006 (mean ± 1 SE; plants with flowers: 2.50 ± 0.56 spiders; plants without flowers: 1.37 ± 0.30 spiders) and 2008 (plants with flowers: 0.50 ± 0.19 spiders; plants without flowers: 0.57 ± 0.17 spiders) (Table 1). The covariate (number of leaves) differed statistically (Table 1), indicating that the number of leaves, and not presence of flowers, determines spider distribution. Multiple linear regressions showed that the distribution of *Peucetia* over the year was related to the number of arthropods in December 2005, May and October ($P \leq 0.032$), as well as number of leaves in February and July ($P \leq 0.026$), and height of plants in December 2006 ($P < 0.001$) (Table 2).

Vertical distribution among ages classes.—In December 2005 adults and subadults of *Peucetia* occurred on higher sites on the crown than juveniles and young (Fig. 1; $F_{3,86} = 6.92$; $P < 0.001$).

DISCUSSION

Peucetia flava occurred only on *Rhyncanthera dichotoma*. This result suggests that in our study site the spider species is strictly associated with this glandular plant. On *R. dichotoma*, these spiders were frequently seen foraging, feeding and displaying reproductive behaviors; females produced egg sacs in almost all months (J.C. Morais-Filho & G.Q. Romero, unpub. data). These observations suggest that *Rhyncanthera* is a suitable microhabitat for *P. flava*. In addition, in northeast, southeast, and southern Brazil *P. flava* is reported to occur associated with sixteen glandular shrubs (Vasconcellos-Neto et al. 2007), thus reinforcing the hypothesis of a high fidelity of

Table 1.—ANCOVA examining the influence of presence/absence of flowers (treatment) on *R. dichothoma* on the abundance of *P. flava*, during two reproductive periods of the host plant (years of 2006 and 2008).

Source of variations	*df*	MS	*F*	*P*
No. of leaves (cov)	1	1.3892	32.59	< 0.001
Treatment	1	0.0123	0.29	0.592
Year	1	0.0298	0.70	0.406
Year × Treatment	1	0.0371	0.87	0.354
Error	66	0.0426		

these spiders to glandular plants. The reason why *P. flava* is found associated with these plants may be due to the function of the glandular hairs as insect traps, which facilitate prey capture by trapping or preventing insects from dislodging themselves and escaping (Dolling & Palmer 1991; Ellis & Midgley 1996; Romero & Vasconcellos-Neto 2004a). In fact, *Peucetia flava* can feed on insects stuck to glandular trichomes of *Rhyncanthera* (e.g., ants, Chironomidae, Aphididae) (J.C. Morais Filho, pers. obs.) and Romero et al. (2008) showed that this spider can also feed on insects stuck to glandular trichomes of *Trichogoniopsis adenantha*. Furthermore, while glandular trichomes could benefit spiders by facilitating prey capture, the spiders preying on these plants may remove phytophagous insects thus also providing benefits to the plants. This hypothesis will be tested in future research.

Generally, spiders occur more frequently on plant parts that have flowers (reproductive branches), since these structures attract potential prey (pollinators) and are thus better quality sites (Louda 1982; Morse & Fritz 1982; Romero & Vasconcellos-Neto 2004a, 2006). However, this seems not to be the case for *P. flava*; although flowers of *R. dichotoma* attract potential prey of *P. flava*, there was no evidence that *P. flava* chose plants based on presence of flowers. These results suggest that *P. flava* chose plants primarily based on presence of glandular trichomes, and not presence of flowers, and reinforces the assumption described above regarding the specific association of this species with glandular plants.

Table 2.—The coefficient (and *P* values in parenthesis) of multiple linear regressions between *P. flava* density (dependent variable) and plant height, number of leaves and total number of arthropods on the plant *R. dichotoma* in different periods of the year. Significant *P* values are boldfaced.

Months	Height	Leaves	Arthropods
December	0.74 (0.064)	0.32 (0.091)	0.27 (**0.032**)
January	−0.20 (0.674)	0.44 (0.090)	0.06 (0.793)
February	0.21 (0.676)	0.60 (**0.003**)	0.22 (0.117)
March	0.60 (0.362)	0.35 (0.182)	0.22 (0.143)
April	−0.90 (0.424)	0.81 (0.059)	−0.22 (0.496)
May	1.51 (0.348)	−0.23 (0.577)	0.59 (**0.029**)
June	0.45 (0.556)	0.37 (0.115)	−0.01 (0.942)
July	−0.13 (0.851)	0.60 (**0.026**)	−0.01 (0.952)
August	0.49 (0.440)	0.36 (0.208)	0.40 (0.080)
September	0.16 (0.768)	0.50 (0.075)	−0.02 (0.896)
October	0.57 (0.319)	−0.33 (0.236)	0.40 (**0.023**)
November	−0.48 (0.445)	0.63 (0.249)	0.18 (0.652)
December	1.17 (<**0.001**)	0.21 (0.297)	0.19 (0.185)

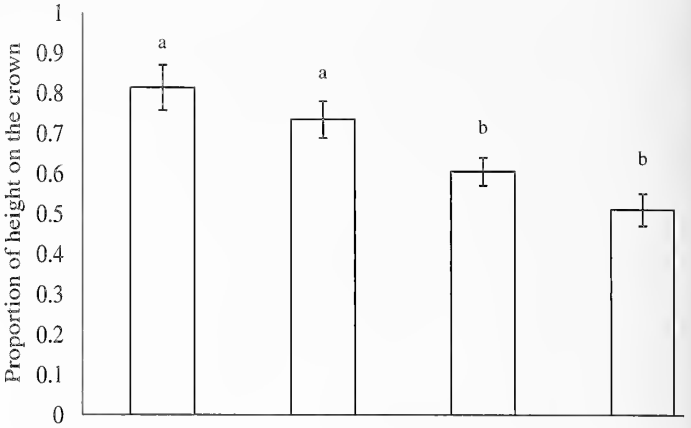

Figure 1.—Vertical distribution of spider age classes in December 2005. Different letters indicate statistical differences (ANOVA/Fisher LSD). Error bars indicate ± 1SE. See age group definitions in Methods.

These results suggest that, in different periods of the year, *P. flava* may be choosing plants based on other characteristics such as the number of arthropods stuck on glandular trichomes, the number of leaves on the plant, or the height of the plant. Plants with more leaves may represent sites of better quality for foraging (larger surface area) and shelter (e.g., Gunnarsson 1990; Romero & Vasconcellos-Neto 2005b). In addition, since leaves of this plant bear glandular hairs able to trap insects, more leaves may mean higher probability of an insect adhering to these sticky structures. In fact, the number of leaves influenced the abundance of adhered arthropods on *R. dichotoma* (J.C. Morais-Filho & G.Q. Romero, unpub. data). Since *P. flava* and its congener *P. rubrolineata* can act as scavengers (Romero et al. 2008), being on plants with greater number of leaves may increase the chance to feed on dead insects stuck to glandular trichomes.

In USA and Mexico *Peucetia viridans* Hentz 1832 is reported to occur associated with the glandular plants *Haplopappus venetus* (Asteraceae) (Louda 1982) and *Cnidoscolus aconitifolius* (Euphorbiaceae) (Arango et al. 2000), respectively. These authors reported that the spider selected the highest plants. Arango et al. (2000) found that *P. viridans* uses high-quality portions of its habitat, choosing those plants offering better sources of food, shelter, and favorable environmental conditions. The frequency of spiders on higher plants could be related to prey availability, as higher plants have a higher number of leaves.

Adults and subadults of *P. flava* occurred on higher sites in the crown than juveniles and young. This distribution may confer an easy way for adults and subadults to migrate by ballooning between plants to search for sites of better quality. Alternatively, higher regions in the canopy may represent sites with higher prey availability. In contrast, younger individuals of *Peucetia* (i.e., juveniles and young) may have selected lower sites possibly as shelter, as well as to avoid competition or cannibalism with the larger conspecifics. In fact, we observed cannibalism in this spider population. In California, Turner (1979) reported that 5.8% of the diet of *P. viridans* was composed of other individuals of *P. viridans*. In contrast to our results, for the *P. viridans* – *C. aconitifolius* system,

Arango et al. (2000) found no preference for location in the plant crown among instars. Thus, although it is expected that larger spiders occur on higher sites and smaller spiders occur on lower ones, this distribution pattern was inconsistent among spider-plant systems, as well as among different periods of the year for our system.

In conclusion, *Peucetia flava* occurred strictly associated with *Rhyncanthera dichotoma* probably due to the presence of glandular trichomes; it may benefit from insects adhering to these sticky structures. On this plant species *Peucetia* seemed to evaluate varying plant parameters depending on the period of the year, being affected mainly by abundance of leaves. Once upon a plant with more leaves, the spiders increase the chance of feeding on dead insects stuck to glandular trichomes through scavenging behavior. Juveniles and young *Peucetia* tended to occur on lower regions on the crown, possibly as a way to avoid competition and cannibalism with the larger conspecifics.

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On the ultrastructure and identity of the eyes of Cyphophthalmi based on a study of *Stylocellus* sp. (Opiliones, Stylocellidae)

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Abstract. The laterally positioned eyes of stylocellid mite harvestmen are simple ocelli composed of a uniconvex cuticular lens, a lentigen layer, a retina, and a layer of pigment cells. Basal laminae separate the lentigen layer (preretinal membrane) and the pigment layer (postretinal membrane) from the retina. The retina is composed of retinular cells and glial cells. The optic nerve comprises mostly afferent axons formed by the retinular cells, which are accompanied by glial cells. Likely there are also few efferent axons. The retinular cells are characterized by their peculiar nuclei, numerous granules and indications of high membrane turnover. A prominent central region of the eye shows numerous, but poorly ordered interdigitations of long microvilli-like processes presenting a poorly developed closed rhabdom. A smaller region with microvilli forming a rather disordered, open rhabdom is located opposite to the lens. The retina is proximally and laterally surrounded by pigment cells containing, in addition to the usual dense granules, some crystalline inclusions, which may act as a tapetum. Hence, the retina seems to be composed of a proximal part and a distal part with two differently organized simple rhabdoms. The eyes of *Stylocellus* thus show basically the same organization as the median (primary) eyes of other Opiliones and are likely laterally displaced median (primary) eyes. The occurrence of these primary eyes in Stylocellidae (and Pettalidae) strengthens the idea that the presence of median eyes is thus a plesiomorphic character of these cyphophthalmid harvestmen.

Keywords: Arachnida, median eyes, mite harvestmen, primary eyes

Opiliones or harvestmen are generally characterized by a pair of dorso-medially positioned eyes often located on a distinct tubercle (e.g., Purcell 1894; Scheuring 1914; Kaestner 1935; Pinto-da-Rocha et al. 2007). However, the members of the suborder Cyphophthalmi (mite harvestmen) were thought to be eyeless with the remarkable exception of most Stylocellidae, possessing a pair of laterally positioned eyes in front of the ozophores bearing the opening of the defense glands (Juberthie 1964; Martens 1978; Shear 1993a,b; Giribet & Boyer 2002; Giribet et al. 2002). Earlier descriptions of eyes located on the ozophores of *Cyphophtalmus duricorius* Joseph 1868 (Sironidae) by Joseph (1868) and Janczyk (1956) turned out to be based on misinterpretations caused probably by the lid-like structure covering the opening of the defense glands which might have been mistaken as a lens or cornea (e.g., Juberthie 1964; Gutjahr et al. 2006). Most members of the cyphophthalmid Pettalidae also bear a pair of eyes but incorporated into the base of the ozophore, or even inside, i.e., located under the integument of the ozophore without a lens (Sharma & Giribet 2006; Boyer & Giribet 2007).

The exceptional position of these eyes in some Cyphophthalmi is enigmatic and raises the question of homology with respect to other eyes in Opiliones. Clarifying the homology of the stylocellid eyes is not a trivial task (see also Sharma & Giribet 2006). Embryology evidently shows that the medially positioned eyes of most Opiliones are true median (primary) eyes (Moritz 1957; Muñoz-Cuevas 1981). Since Cyphophthalmi is now regarded as the sister group to all other Opiliones (Shultz 1998; Giribet et al. 1999, 2002), it may be questioned whether these stylocellid (and pettalidid) eyes are displaced median eyes or whether they are true lateral eyes retained only in these groups (Stylocellidae and Pettalidae) as a plesiomorphy (Shear 1993b; Giribet et al. 2002). As a contribution towards solving this fundamental problem, the eyes of a stylocellid species were investigated here for the first time using light and electron microscopy.

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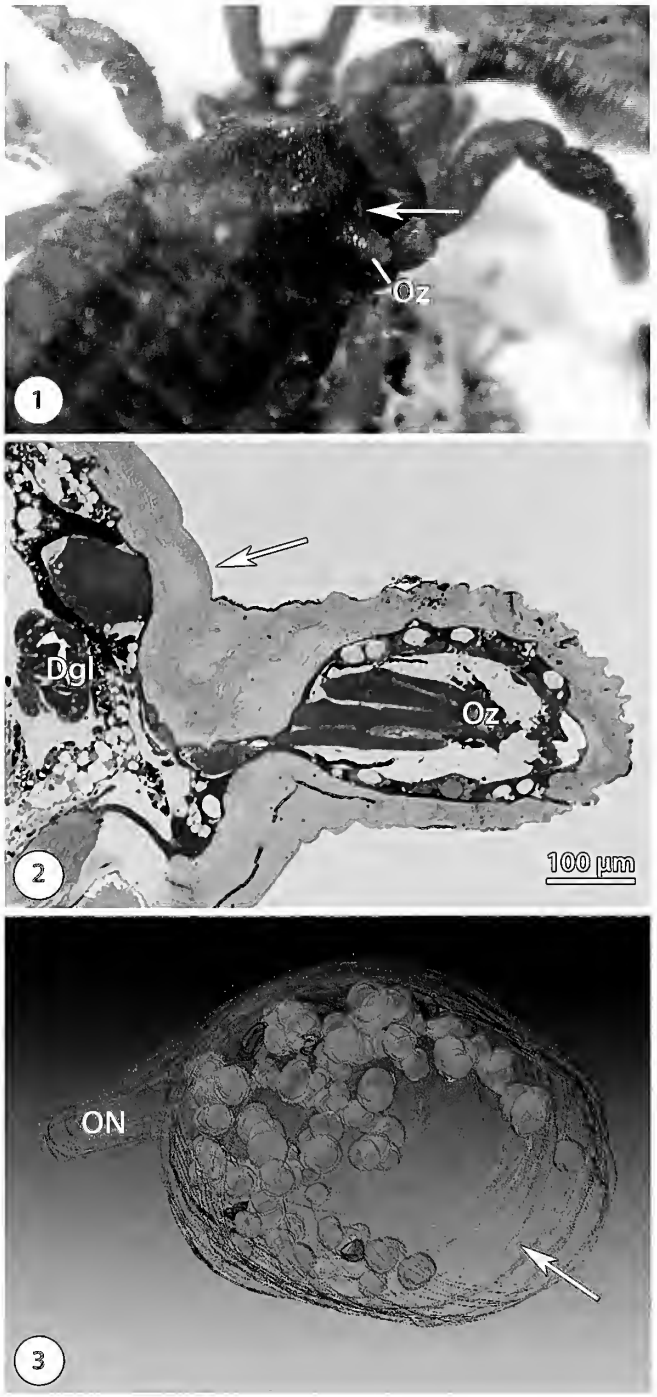
METHODS

Two males of *Stylocellus* sp. collected in Thailand (Krabi Province, Khao Phanom Bencha National Park, rain forest, 22.VII.2005, 8°14′19.9″N, 98°55′11.0″E) by P. Schwendinger were, after videotaping, cut into pieces with a razor blade and fixed in cold 3.5% buffered glutaraldehyde (phosphate buffer pH 7.4; 0.1M) for about 2 h. A 2%, buffered OsO_4-solution for another 2 h was used for post-fixation. The specimens were then dehydrated in graded ethanol series and embedded in Araldite. Ultrathin sections (70 nm) were obtained with a Leica-Ultracut using a diamond knife. Sections were stained with uranylacetate and lead citrate. Semithin sections (400 nm) stained according to Richardson et al. (1960) were used for general orientation with a light microscope Olympus BX60 with digital camera DP 10 (LM). A JEOL JEM-1011 transmission electron microscope (TEM) was used for examining the sections. For 3-D reconstruction Amira software (Mercury Computer Systems GmbH) was used. One specimen, fixed in the same way as the one used for TEM, was studied after critical point drying with a Zeiss DSM 940A scanning electron microscope (SEM).

RESULTS

In the living animals, the eyes are distinct and shiny due to their almost smooth lenses, which slightly project (Figs. 1, 4). Sections through the eyes reveal that they are prominent, nearly spherical structures comprising a uniconvex cuticular



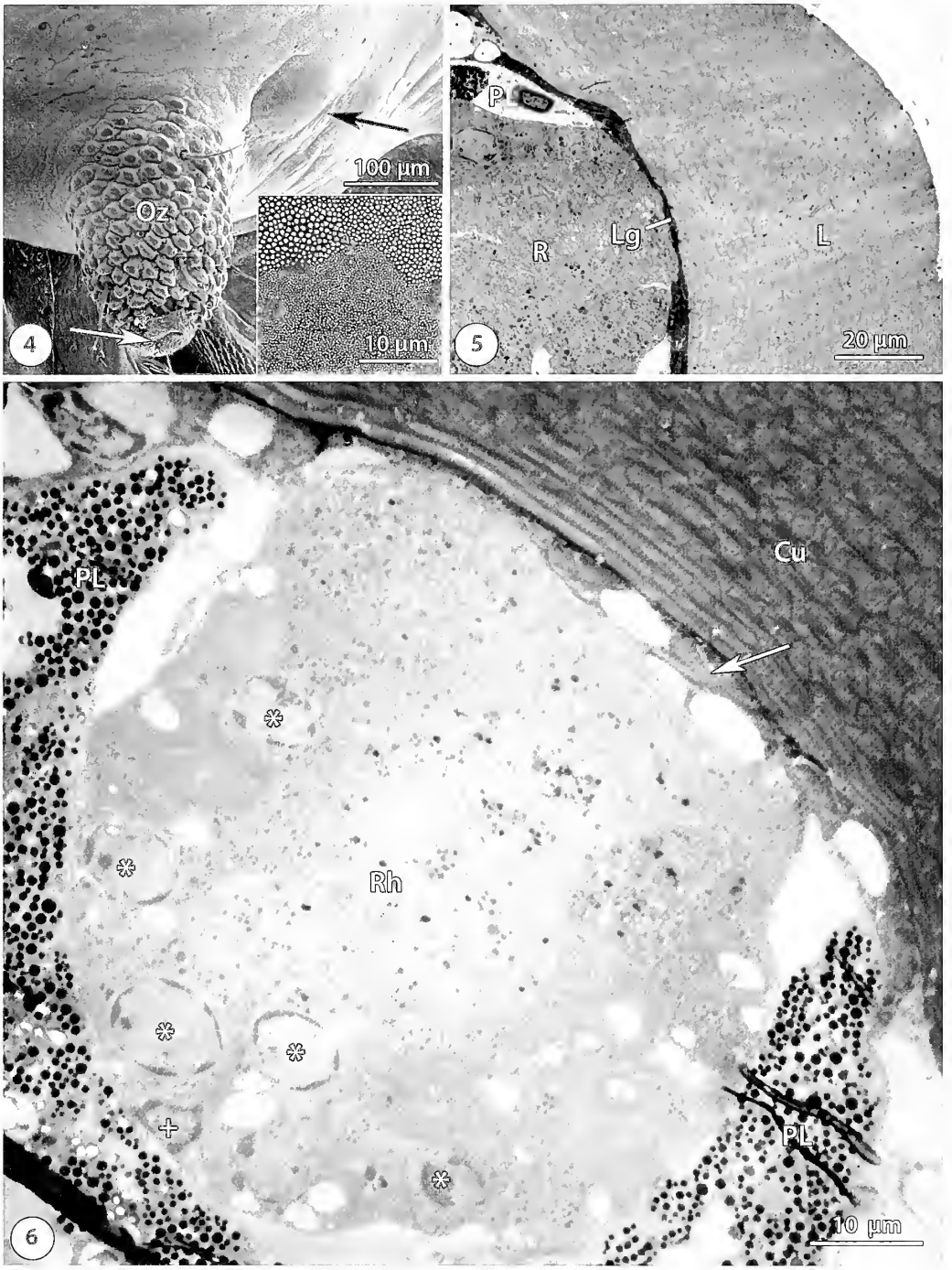
Figures 1–3.—*Stylocellus* sp.: 1. In the living specimen, the eyes are distinct and shiny due to their prominent lens (arrow) in front of the ozophore; 2. LM of a section through ozophore and eye (arrow). The eye is a prominent, nearly spherical structure comprising a uniconvex cuticular lens, a group of cells forming the sensory part, i.e., the retina. The latter is partly surrounded by a layer of pigment cells containing numerous mostly densely staining granules. Note that these granules also occur distant from the eye, though less abundantly; 3. 3-D-reconstruction of retina showing arrangement of nuclei of retinular cells (yellow) and glial cells (blue). Arrow indicates direction of incidence of light. The center of the retina is mainly occupied by the distal rhabdom (compare Figs. 6, 13, 14). The location of the proximal rhabdom is close to the origin of the optic nerve. Dgl = defense gland; ON = optic nerve; Oz = ozophore.

lens, a thin electron-dense lentigen layer and a group of cells arranged spherically forming the sensory part, i.e., the retina. The latter is partly surrounded by a thick layer of pigment cells containing numerous mostly densely staining granules. The optic nerve leaves the structure penetrating this latter layer (Figs. 2, 3, 19).

Lens.—The slightly projecting lens is composed of multilayered cuticle (thickness: about 50µm) which appears hardly modified when compared to the adjacent cuticle (Figs. 5, 6). The cuticle seems to be strongly sclerotized. A very thin epicuticle is found (Fig. 5). The outer surface of the lens is covered with protuberances, which are slightly smaller than those found in adjacent parts (Fig. 4, inset).

Lentigen layer.—The lentigen layer is composed of flat, densely staining cells containing densely staining nuclei. A thin basal lamina is present (Figs. 5, 7). The lentigen layer is continuous with the epidermal layer (Figs. 2, 6).

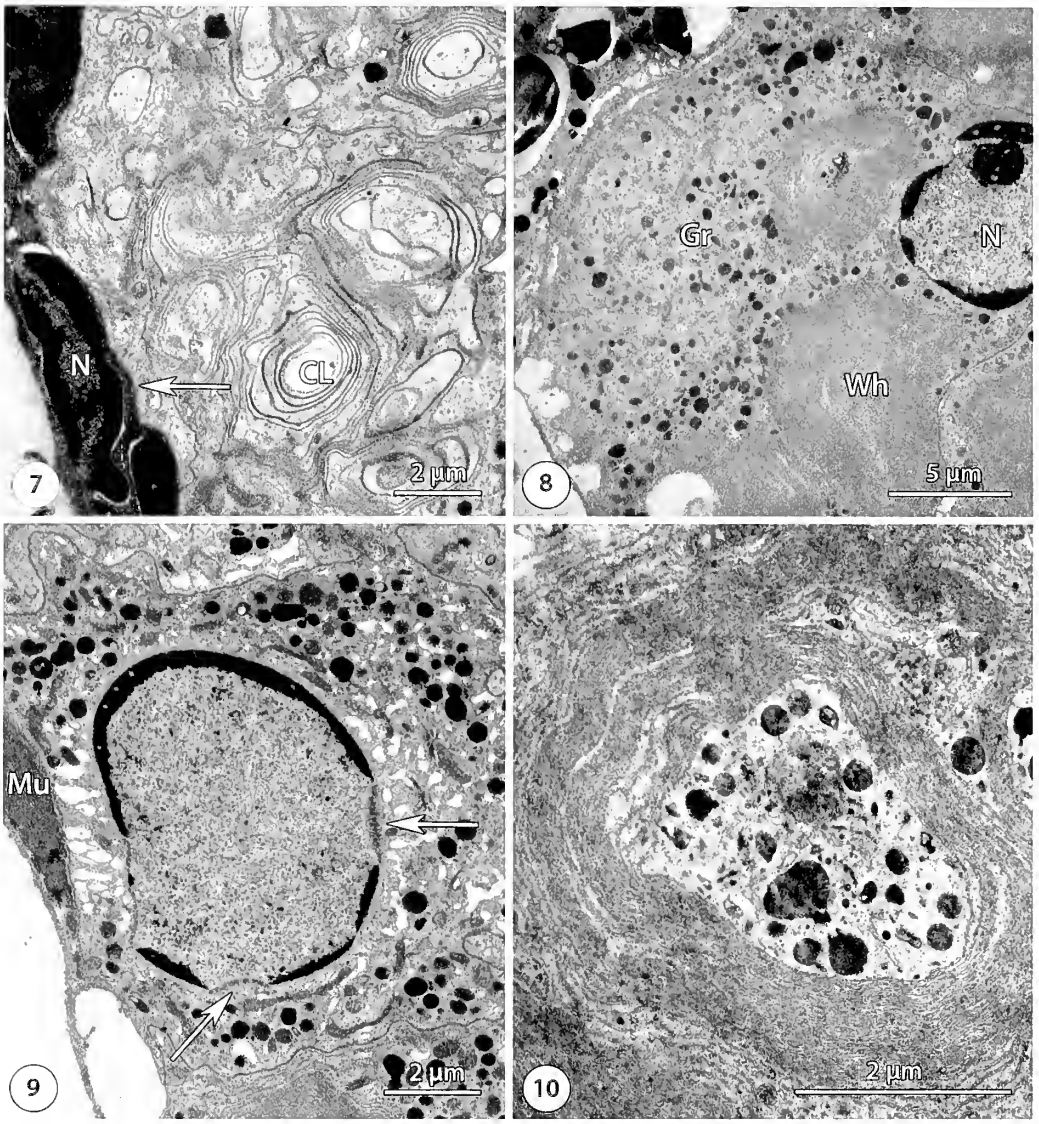
Retina.—The nearly hemispherical retina is composed of a layer of epithelial retinular cells containing basally (or peripherally) located nuclei with a distinctive arrangement of heterochromatin (Fig. 6). The patches of heterochromatin are attached to the nuclear envelope, which here does not show nuclear pores, and they are regularly interrupted by heterochromatin-free regions (Figs. 8, 9, 19). In these latter regions many nuclear pores are located (Fig. 9).These nuclei are not found in the region of the retina directed toward the lens (Figs. 3, 5). Adjacent to the nuclei, conspicuous and quite large whorls of membranes occur. In the center of these whorls, dense granules are frequently located (Figs. 8, 10). In this nuclear region and slightly towards the center of the retina, the cells contain many moderate-densely staining granules, which originate from small Golgi bodies (Fig. 11). Further centrally, the cytoplasm of these cells is dominated by numerous cisterns or lamellae arranged (in the sections) in circles, which frequently contain more of such circles. It seems that some of the dense granules come into contact with these cisterns and may discharge their contents in the space between the membranes (Figs. 7, 12). There are also cytoplasmic processes interdigitating with similar structures of a neighboring cell (Figs. 13, 14). Though a regular arrangement of rhabdomeric microvilli was not found, we postulate that this area represents a simple closed rhabdom. Furthermore, a small area of irregularly arranged microvilli which are provided by cells similar to those just described was found rather close to the origin of the optic nerve (Figs. 15, 16). In this region, representing a rather disordered open rhabdom, centrioles were found (Fig. 17 inset). The retinular cells are connected by small zonulae adhaerentes (Fig. 16). The optic nerve is composed of processes of the retinular cells which are found at the periphery of the structure converging upon the origin of the nerve (Figs. 17, 19, 21). In addition to these retinular cells which are easily recognized because, e.g., of the very peculiar nuclei, we found a few nuclei which were distinctly smaller and more dense (Figs. 3, 6, 19). These nuclei likely belong to glial cells which extend with flat processes between the retinular cells. Similar nuclei were also found in the optic nerve. Rarely small cell processes were observed containing small vesicles. These processes likely represent nerve endings (Fig. 18). The retinular cells may differ with regard to electron-density of their cytoplasm. They are also partly shrunk with distinct intercel-



Figures 4–6.—*Stylocellus* sp.: 4. SEM of ozophore with opening of defense gland (white arrow) and lens (black arrow). Inset: border between lens and adjacent cuticle. Note distinctly smaller tubercles on the cuticular lens; 5, 6. TEM: 5. The lens slightly projects and is composed of about 20 layers of endocuticle and an almost homogeneous exocutiele whieh appears hardly modified when compared with the adjacent cuticle (see Fig. 6). The thin epicuticle is provided with small tubercles (compare Fig. 4). The lentigen layer is continuous with the epidermal layer; 6. Overview showing cuticle adjacent to the lens, epidermal layer (arrow), retina and pigment layer. * nuclei of retinular cells; + nucleus of glial cell. Cu = cutiele; L = lens; Lg = lentigen layer; Oz = ozophore; PL = pigment layer; R = retina; Rh = region of distal rhabdom.

lular spaces running between each other. Such differences may reflect different physiological phases. The retina is surrounded by a thin basal lamina. In one of the eyes we observed a thin cross-striated muscle fiber (Figs. 9, 20) between the basal lamina and the layer of retinular cells.

Pigment layer.—Pigment cells are not only found surrounding the retinular cells, but also distant from the eye. These cells are evidently derived from connective tissue or fat bodies. However, they are distinctly concentrated around the retinular cells leaving free only the part of the retina under the lens. The pigment cells are dominated by very densely staining granules, which surround a moderate to densely staining ovoid cytoplasm and nucleus (Figs. 2, 6, 19). However, there are also larger electron-lucent inclusions or small vacuoles containing irregu-



Figures 7–10.—*Stylocellus* sp. TEM: 7. The lentigen layer is composed of flat densely staining cells containing densely staining nuclei. A thin basal lamina is present (arrow). Note circles of membranous lamellae in retinular cell; 8. Overview of peripheral part of retina showing nucleus with peculiar chromatin pattern and whorls of membranes; 9. Close up of peripheral region of retina with nucleus. Note nuclear pores (arrows) and granules. Between postretinal membrane (basal lamina) and retinula cell, a small muscle cell is found; 10. Conspicuous whorl of membranes with dense granules. Cl = circles of membranous lamellae; Gr = granules in retinular cells; Mu = muscle cell; N = nucleus; Wh = whorl of membranes.

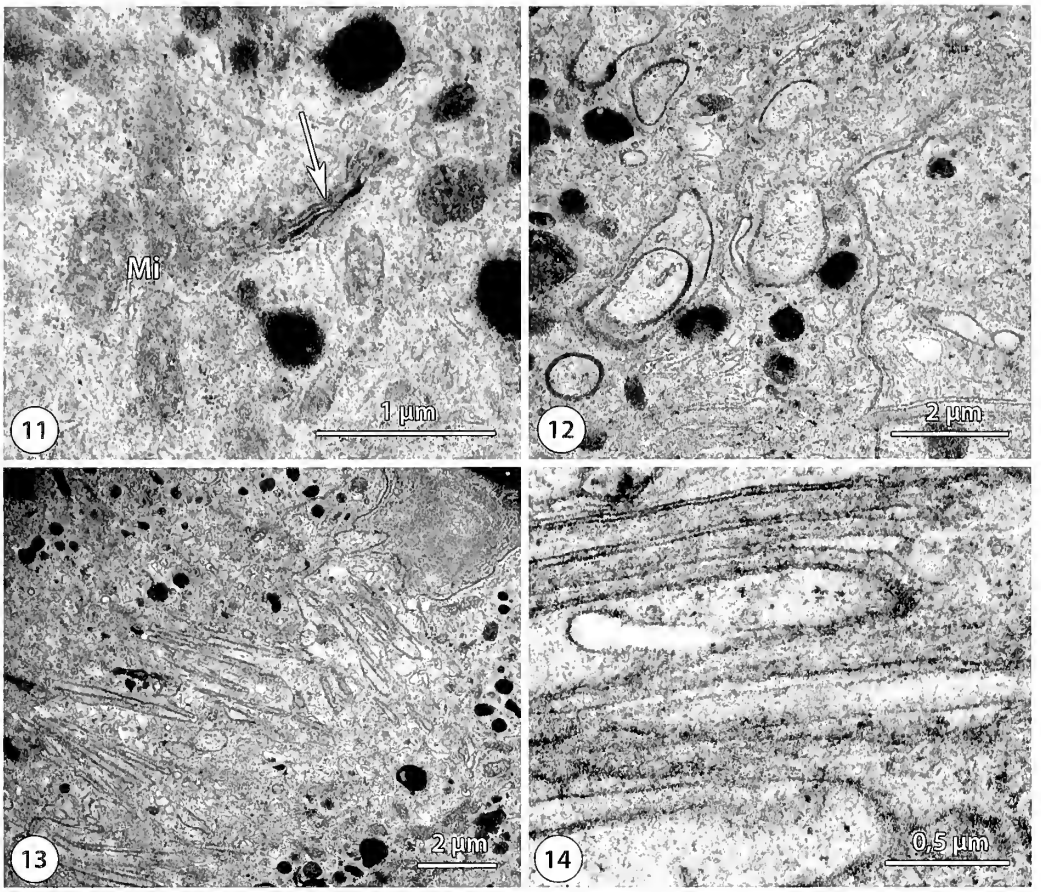
larly shaped components. Furthermore, some of the inclusions seem to contain crystalline material. These latter inclusions are found only opposite to the lens (Fig. 20). The layer of pigment cells is bordered by a thin basal lamina.

A few cells of unknown function are found between the basal lamina of the pigment cells and the basal lamina surrounding the retina. A small trachea enters the pigment layer.

Optic nerve.—The optic nerve leaves the retina at the posterior inner border of the eye (Figs. 3, 19). It penetrates the layer of pigment cells and is composed of more than 40 axons (Figs. 19, 21). The axons are moderately densely stained and contain numerous microtubules, some mitochondria and occasionally also some of the granules described from the retinular cells (see above). The axons are accompanied and surrounded by extensions of glial cells, which are more electron-lucent than the axons themselves. A thin basal lamina surrounds the nerve. A small trachea runs along with the nerve but outside its basal lamina (Fig. 21).

DISCUSSION

Extant Arachnida typically have one pair of median (primary) eyes and up to five pairs of lateral (secondary) eyes (Paulus 1979, 2004; Weygoldt & Paulus 1979; Giribet et al. 2002) classified as ocelli. Exceptions are, besides Opiliones (see below), Pseudoscorpiones (Weygoldt 1969), and anactinotrichid mites (Anactinotrichida = Parasitiformes s.l.) (Alberti 2006; Dunlop & Alberti 2007), which have no median eyes, and the eyeless Palpigradi. The extant Ricinulei are usually considered to lack eyes although they bear more or less distinct light spots on the cuticle that may be associated with light reception. A similar situation is found in Schizomida (e.g., Moritz 1993).

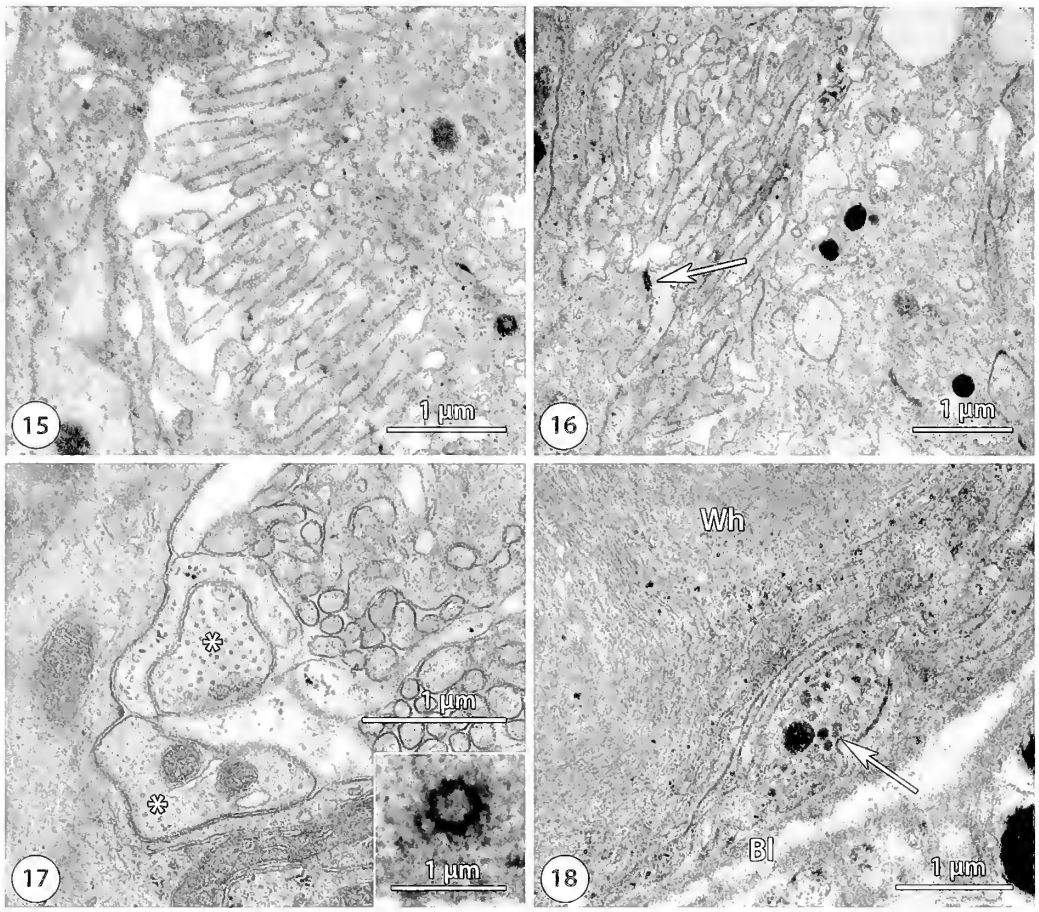


Figures 11–14.—*Stylocellus* sp. TEM: 11. Dense granules in the retinular cells are produced by small Golgi bodies (arrow); 12. Close to the center of the retina (compare Figs. 3, 5, 6) circles of membranous lamellae are frequent; 13. Overview showing the interdigitations of the poorly developed distal, closed rhabdom; 14. Close up of the distal rhabdom with interdigitating rhabdomeric microvilli-like projections of retinular cells. Mi = mitochondria.

The presence of laterally positioned eyes in Cyphophthalmi is remarkable for two reasons. First, presence of eyes in this group was, until recently, regarded as exceptional, being restricted to some species of Stylocellidae (the detection of eyes in Pettalidae as reported above makes this less peculiar). Second, the lateral position of these eyes is remarkable since eyes of Opiliones are usually located medially and are frequently referred to as median eyes (e.g., Kaestner 1935; Paulus 2004), although several cases of a lateral migration of the median eyes are known in Laniatores. Hence the question with regard to Stylocellidae (and Pettalidae) is whether these eyes represent lateral eyes homologous to those occurring in most of the other Arachnida or whether these eyes are displaced median eyes, as is the case in the abovementioned derived Laniatores, as already discussed by Juberthie (1964). However, Shear (1993a, b) homologized stylocellid eyes with arachnid lateral eyes because of the presence of a tapetum indicative of many lateral eyes; a tapetum is always lacking in median eyes. This interpretation of the stylocellid eyes was accepted by Giribet et al. (2002). Another possibility could be that these eyes are secondarily evolved, as those detected in oribatid mites (Alberti & Fernandez 1988). The evidence presented here refutes this latter hypothesis.

The eyes of *Stylocellus* sp. are largely composed of the same components as the median eyes of other Opiliones (e.g., Purcell 1894; Scheuring 1914; Juberthie 1964; Curtis 1970; Schliwa 1979; Meyer-Rochow & Liddle 1988). These authors observed cuticular lenses, which are often biconvex, contrasting with the simple uniconvex lens of *Stylocellus*. A vitreous (glassy) body is located under the lens, which is comprised of a modified epidermal layer and hence corresponds to the less modified lentigen layer in *Stylocellus*. A pronounced vitreous body is evidently not developed in *Stylocellus*. The preretinal and postretinal membranes correspond to the basal laminae of the lentigen layer, retina and pigment cell layer. The retina of *Stylocellus* evidently is comparable to the more complex retina of other harvestmen. As in other Opiliones there is a conspicuous layer of pigment cells.

Peculiarities of the *Stylocellus* eyes are mainly found in the retina, which unfortunately is yet not completely understood based solely on the studied material. The reason for this is the peculiar arrangement and shape of retinular cells, which do not show an evident regular organization of the retina, and the limited material available for this study. At present we can distinguish two cell types, retinular cells (receptor cells) and glial cells (corresponding probably to the sheath cells of Schliwa 1979). We could furthermore recognize distinct regions in the retina: a nuclear region with conspicuous whorls of membranes and numerous dense granules, a region characterized by many membranes or lamellae and interdigitations between neighboring cells. These interdigitations may

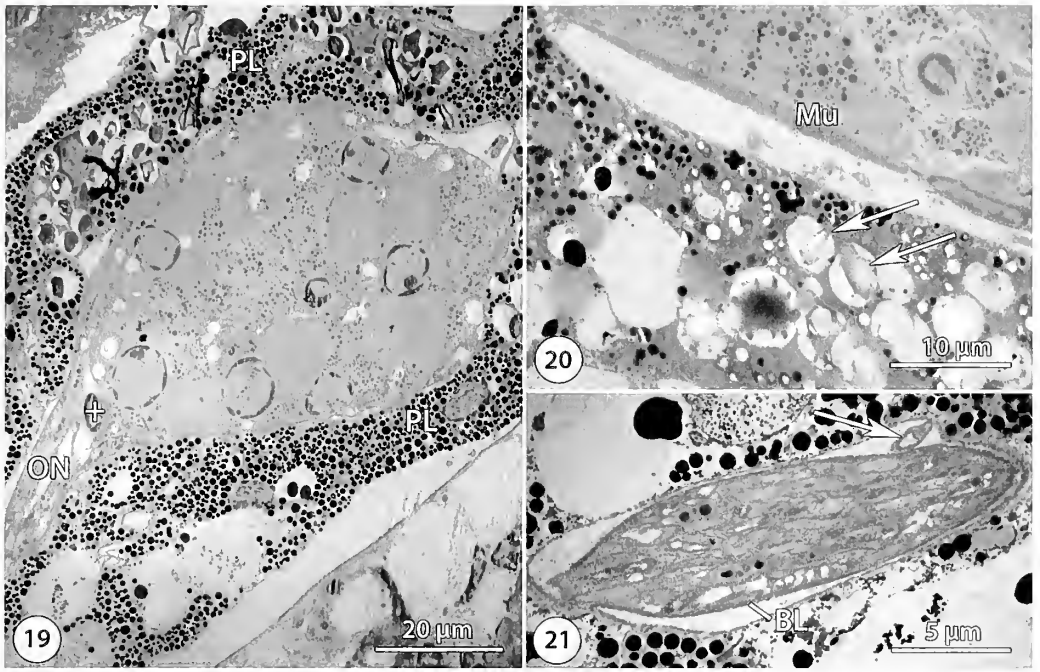


Figures 15–18.—*Stylocellus* sp. TEM: 15. The proximal, open rhabdom; 16. Another detail of the proximal rhabdom with irregularly arranged microvilli. Arrow points to small zonula adhaerens. 17. Axons (*) close to the proximal rhabdom. Inset: Centriole observed in retinular cell; 18. Putative efferent nerve ending (arrow) at the base of a retinular cell. Bl = basal lamina (postretinal membrane); Wh = whorl of membranes.

be regarded as forming a poorly developed closed rhabdom. Finally we found a region with distinct, but irregularly arranged microvilli forming a rather disordered, open rhabdom. Remarkably, this latter part of the retina is not found close to the lens but, instead, opposite to it, close to the origin of the optic nerve, suggesting an inverse (indirect) orientation. The retina thus shows a differentiation into a distal and a proximal part with a distal, closed and everse rhabdom and a proximal open and inverse rhabdom. However, we could not yet discriminate different types of retinular cells, i.e., (proximal) retinular cells and distal retinular cells, contributing to these rhabdoms (see Schliwa 1979). All the retinular cells show similar ultrastructure, except for varying cytoplasmic densities as mentioned above. We also could not detect the arhabdomeric (or eccentric) cells known from other Opiliones, as well as from other chelicerates including *Limulus* (e.g., Fahrenbach 1975, 1999; Fleissner & Siegler 1979; Schliwa 1979; Kaiser & Alberti 1991; Alberti & Coons 1999). However, the few processes representing putative nerve endings may indicate an efferent innervation known also from other chelicerate eyes, which have been shown to induce the movements of pigment granules according to a circadian clock in scorpions (Fleissner & Schliwa 1977; Fleissner 1986). Displacement of pigments as an adaptation to varying light intensities has long been known from, e.g., spiders and may also be induced through stimuli by these efferent nerves (e.g., Scheuring 1914; Fahrenbach 1999). Membranous cisterns or lamellae have also been described from other arachnid eyes including Opiliones (e.g., Schliwa 1979). In *Stylocellus* the very conspicuous whorls of membranes in the nuclear region are most remarkable. We suggest that all these membranous structures are signs of a high membrane turnover, probably related to circadian changes of sensitivity as reported from other chelicerates (e.g., Blest 1978; Fleissner 1986; Fahrenbach 1999).

A remarkable feature is the presence of different types of granules in the pigment cells. Besides densely staining pigment granules, there are lucent granules containing irregular inclusions or even crystalline material. These inclusions seem to be concentrated in the background of the eye and may represent a tapetum (corroborating Shear's observation 1993a, b) and thus correspond to the peculiar positioned proximal, open rhabdom of the retina (see above). Presence of a tapetum is interpreted as an adaptation to nocturnal life, but may also be advantageous to species living in cryptic environments, as is the case of Cyphophthalmi. It is lacking, e.g., in the diurnal jumping spiders (Eakin & Brandenburger 1971).

It can be concluded that the eyes of *Stylocellus* largely correspond structurally to those known from other Opiliones, though being much simplified. In contrast to other eyes



Figures 19–21.—*Stylocellus* sp. TEM: 19. Overview of eye showing origin of optic nerve; + indicates nucleus of glial cell; other nuclei belong to retinular cells (compare Figs. 6, 8, 9); 20. Part of pigment layer opposite the incident light showing peculiar inclusions that might serve a tapetum function. Arrows point to crystal-like inclusions. However, a distinct tapetum layer is not present; 21. Oblique section through optic nerve composed of about 40 axons. Arrow points to small trachea. BL = basal lamina; Mu = muscle cell; PL = pigment layer.

described from harvestmen, *Stylocellus*' eyes appear to present a partly inverse retina directed towards a tapetum suggesting that these eyes might really represent lateral (secondary) eyes (Shear 1993a, b). However, the tapetum of *Stylocellus* differs strikingly from the tapeta known from spiders, whip scorpions and whip spiders, or the early derivative opilioacarid mite *Neocarus texanus* (Chamberlin & Mulaik 1942). In these taxa, tapeta represent distinct layers of specialized cells containing flat crystalline material (Scheuring 1914; Baccetti & Bedini 1964; Homann 1971; Meyer-Rochow 1987; Kaiser & Alberti 1991; Weygoldt 2000). This is evidently not the case in *Stylocellus*. Here the putative tapetum is simply a modification of certain pigment cells. Tracing the optic nerve into the brain may help to solve this problem of eye homology in *Stylocellus*. Also clarifying embryonic development of the eyes would be helpful. Do they develop by invagination as the typical median eyes of Chelicerata including Opiliones (Moritz 1957; Paulus 1979, 2004)? In any case it is evident that the presence of eyes in most Stylocellidae (and most Pettalidae) is a plesiomorphic character within Cyphophthalmi (Sharma & Giribet 2006; Boyer et al. 2007), and therefore the lack of eyes in all members of the families Neogoveidae, Ogoveidae, Sironidae and Troglosironidae must be a derived adaptation to a cryptic mode of life pretty much limited to the leaf litter environments, caves, or the soil.

Following our observations, which did not show fundamental differences in the laterally positioned eyes of *Stylocellus* with those of Phalangida, the interpretation that median (primary) eyes moved laterally in the evolution of Cyphophthalmi and later disappeared in most taxa of mite harvestmen seems most likely to us. In accord with the study of Muñoz-Cuevas (1981) on eye regression in *Ischyropsalis* species, the simplified lens and the absent vitreous body may be regarded as signs of regression in the eyes of *Stylocellus*.

While stylocellid eyes are conspicuous and located in front of the ozophores, pettalid eyes seem to have suffered a process of internalization. Pettalid eyes are, when found, located at the base of the ozophore (e.g., in *Chileogovea*, *Pettalus*, and some *Rakaia*), while species of *Aoraki*, *Austropurcellia*, *Neopurcellia*, and some *Rakaia* have the eyes incorporated into the ozophore (Sharma & Giribet 2006; Boyer & Giribet 2007). This type of eye is only visible in light microscopy, but not appreciated through scanning electron microscopy, as the eye lacks a cuticular lens entirely. Whether this particular pettalid eye is ultrastructurally similar to the stylocellid eye described in this study remains to be determined.

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Success of managed realignment for the restoration of salt-marsh biodiversity: preliminary results on ground-active spiders

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Abstract. Since the early 1990s managed realignment, where formerly reclaimed land is re-exposed to tidal inundation through breaching of coastal embankments, has been increasingly used throughout Northern Europe as a cost effective and sustainable response to biodiversity loss and flood management. This study aimed to evaluate the success of managed realignment schemes that resulted in salt-marsh development for the restoration of spider assemblages. Restoration of salt-marsh fauna was studied by comparing ground-active spiders between recently inundated land (3–14 years old) and pair-matched, adjacent natural salt marshes. Natural reference salt marshes were characterized by a relatively low species richness, the dominance of late-successional stage species such as *Pirata piraticus* (Clerck 1757), and the presence of species preferring a closed vegetation canopy like *Arctosa fulvolineata* (Lucas 1846) and *Pardosa nigriceps* (Thorell 1856). Restored habitats were characterized by greater species richness than in reference habitat and by the presence of halophilic species (*Enoplognatha mordax* (Thorell 1875) and *Erigone longipalpis* (Sundevall 1830)) and abundance of *Pardosa purbeckensis* (Westring 1861). These preliminary results argue for maintaining a maximum of successional stages in salt marshes, as they increase the diversity of halophilic spiders.

Keywords: Araneae, habitat restoration, ecological succession, halophilic species

For centuries, coastal habitats have been impacted by human activity where over-exploitation, habitat modification and pollution have led to loss of biodiversity and ecological resilience (Lotze et al. 2006). Changing climate and weather patterns have accelerated losses in the recent past (van der Wal & Pye 2004). Replacing coastal habitats where they are eroded, inundated or otherwise impacted is particularly important given the high level of ecosystem service they provide. Salt-marsh creeks provide spawning and nursery areas for many fish species and their vegetation provides roosting, nesting and feeding sites for birds. In addition to the specialist flora and fauna directly associated with tidal salt marshes they are areas of high productivity providing a source of organic matter and nutrients for adjacent marine habitats. Since the early 1990s, restoring tidal inundation to formerly reclaimed land, either through a breach in current coastal defences or whole scale embankment removal (managed realignment), has been increasingly used throughout Europe as a cost effective and sustainable response to biodiversity loss and flood management (French 2006).

Re-establishing self-sustaining plant communities are often a primary goal of such restoration efforts as these communities perform many of the biological and economically desirable functions of wetland ecosystems. Results from several managed realignment schemes have shown that with fairly minimal pre-treatment and management by allowing tidal ingress through a simple, relatively small breach, the landward realignment of coastal defences will quickly produce intertidal mudflats on low-lying agricultural land (Garbutt et al. 2006). If the elevation is suitable, mud flats will be colonized by salt-marsh plants. Monitoring programs to date have focused on the restoration of some functions, in particular sediment dynamics, plant colonization, and bird usage (Wolters et al. 2005a), but at the moment nothing is known about the restoration of terrestrial arthropod communities. This fauna represents a special conservation interest as it is currently endangered by numerous direct or indirect human impacts such as diffuse soil pollution from adjacent cultivated fields, eutrophication, and overgrazing (see the review of Adam 2002).

This study aimed to evaluate the success of managed realignment for the restoration of salt-marsh biodiversity and in particular the response of one arthropod community (*Araneae*), which constitutes a major component of the salt-marsh arthropod fauna (e.g., Meijer 1980; Pétillon et al. 2007). Ecological succession is defined as a non-seasonal, directional pattern of species change (Morin 1999). Vegetation succession in salt marshes is the result of the accumulation of nutrients in the soil leading to an increase in plant biomass and changes in species composition (Olff et al. 1997) and the frequency of tidal inundation as determined by elevation. The responses of plants to the habitat conditions found along successional gradients are well known, but few data are available on responses of arthropods. According to current theories on ecological succession and former results on salt-marsh vegetation (e.g., Olff et al. 1997), we expect (i) greater spider species richness in natural sites than in restored sites (i.e., increase in this parameter towards a climax) and (ii) differences in spider populations between natural and restoration sites (i.e., changes in species abundances along successional stages). Both hypotheses will be tested in this preliminary study by comparing ground-active spider assemblages between land recently re-exposed to tidal inundation (3–14 year old) and pair-matched natural salt marshes.

METHODS

Sampling design.—The present study was carried out in the English county of Essex (S.E. England, UK). Sites breached as

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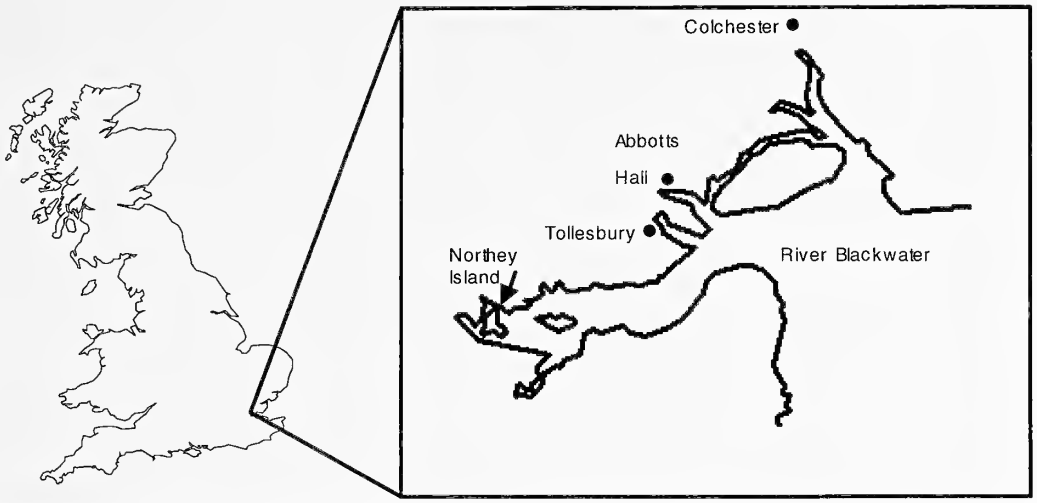

Figure 1.—Location of the 3 study sites (each site contains both restored and natural habitats) along the Blackwater River estuary (English county of Essex, UK).

part of managed realignment schemes were sampled in June 2005 giving several examples of salt-marsh development on former agricultural land. Along the Blackwater River estuary, three sites were selected because they had adjacent, natural areas (Fig. 1): Abbotts hall (Site A, 51°47′10″N, 0°51′00″E, breached 3 years ago), Tollesbury (Site B, 51°45′40″N, 0°50′00″E, breached 10 years ago), and Northey Island (Site C, 51°43′00″N, 0°43′00″E, breached 14 years ago). Sites were arranged as matched pairs with each managed realignment site (coded R for restored site) having an adjacent reference marsh (coded N for natural site) at the same elevation. The natural salt marshes, adjacent to the managed realignment sites, were only separated by the remains of the old embankment and connected by the same creek network.

Spider sampling.—Cursorial spiders were sampled with pitfall traps, consisting of polypropylene cups (8 cm diameter) with ethylene-glycol as preservative. Ten pitfall traps were installed along a 100 m long-transect at each site. Transects were placed at the same elevation (± 0.01 m) within the managed realignment site as that of the adjacent reference marsh using a laser theodolite. The elevation was selected by determining the range of the natural reference marsh by topographic survey, then selecting an elevation at random. Transects were placed parallel to the embankment and were centered on the original breach in the seawall. Elevation was used as a surrogate for tidal inundation to ensure that the arthropod communities within the managed realignment sites and reference marshes received equivalent submergence frequencies, and was checked by observing the depth and extent of the incoming tide for each site. No differences were observed. Pitfall traps were spaced 10 m apart, this being considered to be the minimum distance for avoiding interference between traps (Topping & Sunderland 1992). Data used in this study concerned the first dates of trapping in 2005 from 3–6 June. Catches in pitfall traps were related to trapping duration and pitfall perimeter, which calculates an "activity trappability density" (number of individuals per day and per meter: Sunderland et al. 1995). All the spiders collected were preserved in 70% ethanol, transported to the laboratory for species identification and kept in the University collection (Rennes, France). Nomenclature follows Canard (2005), except for *Pardosa purbeckensis* (see complete taxonomic list: Table 1), absent from this work but now considered to be a valid species (A. Canard pers. comm.).

Data analyses.—The assessment of restoration success was conducted by comparing two conservation criteria, i) abundance of target species and ii) species richness, between newly created and natural areas. The use of stenotopic species is also recommended in studying the impact of human activities and management on arthropod communities (Samways 1993; New 1995; Dufrêne & Legendre 1997). In this study, the target species were halophilic species, defined by their preference or exclusive presence in salt-marsh habitats, and rare species belonging to the Red Data Book and/or the Review of Nationally Notable Spiders of Great Britain (both statuses from Harvey et al. 2002). Halophilic species are able to resist regular submergence by seawater (monthly in Europe) and the resulting high soil salinities (Foster & Treherne 1976; Irmler et al. 2002; Pétillon et al. 2004). Speeies richness is widely used as a conservation target (e.g., Noss 1990; Bonn & Gaston 2005). The success of managed realignment was assessed by applying 2-way ANOVAs (GLM) to species richness and abundances with habitat type (restored or natural), site (A, B, or C) and their interaction (habitat type*site) as factors. In case of non-normal distribution (according to Kolmogorov-Smirnov tests), mean community variables were log-transformed to meet the assumptions of these Factorial ANOVAs.

RESULTS

A total of 291 adult spiders belonging to 7 families and 27 species (see taxonomic list in Table 1) were caught in natural and restored sites in 2005. Five halophilic species were recorded during the study, including two rare species: the lycosid *Arctosa fulvolineata* and the theridiid *Enoplognatha mordax*, respectively listed as Nationally Rare (status RDB3) and Nationally Scarce (status Notable A). The comparison of species composition between restored and natural sites showed a relatively low number of species only found at the natural sites (Table 1). Nine species were shared between natural and restored sites, including the halophilic species *Pardosa*

Table 1.—Taxonomic list, conservation interest (species in bold: interest is based on habitat and/or rarity according to Harvey et al. 2002), and habitat specificity (1: species only found in natural sites; 2: species shared between natural and restored sites; 3: species only found in restored sites) of the spider species.

Species	Interest		Habitat specificity
	habitat	rarity	
Gnaphosidae			
Drassyllus pusillus (C.L. Koch 1833)			3
Linyphiidae			
Bathyphantes gracilis (Blackwall 1841)			2
Diplocephalus permixtus (O. Pickard-Cambridge 1871)			1
Erigone atra (Blackwall 1841)			3
Erigone longipalpis (Sundevall 1830)	x		3
Hypomma bituberculatum (Wider 1834)			1
Oedothorax apicatus (Blackwall 1850)			3
Oedothorax fuscus (Blackwall 1834)			2
Oedothorax retusus (Westring 1851)			3
Pocadicnemis juncea Locket & Millidge 1953			1
Silometopus ambiguus (O. Pickard-Cambridge 1905)	x		2
Tenuiphantes tenuis (Blackwall 1852)			2
Lycosidae			
Arctosa fulvolineata (Lucas 1846)	x	x	1
Arctosa leopardus (Sundevall 1833)			3
Pardosa agricola (Thorell 1856)			3
Pardosa nigriceps (Thorell 1856)			1
Pardosa prativaga (L. Koch 1870)			2
Pardosa purbeckensis (Westring 1861)	x		2
Pardosa palustris (Linnaeus 1758)			2
Pardosa pullata (Clerck 1757)			3
Pirata piraticus (Clerck 1757)			2
Trochosa ruricola (DeGeer 1778)			3
Philodromidae			
Thanatus striatus C.L. Koch 1845			2
Tetragnathidae			
Pachygnatha clercki Sundevall 1823			1
Theridiidae			
Enoplognatha mordax (Thorell 1875)	x	x	3
Robertus arundineti (O. Pickard-Cambridge 1871)			3
Thomidae			
Ozyptila simplex (O. Pickard-Cambridge 1862)			3

purbeckensis and *Silometopus ambiguus*. Twelve species were found only in restored sites, two of which were halophilic: *Enoplognatha mordax* and *Erigone longipalpis*.

GLM revealed significant effects of habitat on total number of individuals, species richness, and on abundances for most species (Table 2). Site had also a significant effect for these species, resulting in several cases of significant interactions between sampling site and habitat type. No significant differences were found between the abundances of three species in natural and restored areas, despite higher abundances of *Pirata piraticus* in natural sites. For this latter, the effect of sampling site was significant and nearly significant for *Tenuiphantes tenuis*.

Total number of individuals and total species richness were higher in restored sites than in natural ones (Fig. 2). Mean values of these parameters significantly differed between sites, being greater in restored sites. Among the most abundant species that could be compared between sites, three (*Pardosa purbeckensis*, *Oedothorax apicatus*, and *O. fuscus*) showed abundances significantly higher in restored sites than in natural ones.

DISCUSSION

Habitat age, habitat structure, and species richness.—In this study, greater species richness was found in restored sites, invalidating our first hypothesis of higher species richness in natural habitats. In accordance to the results of Hurd & Fagan (1992), we suggest that habitat structure determines ground-active spider species richness rather than successional age per se. For example, among the six species only found at natural sites, the presence of at least two lycosid species can directly be related to the presence of a dense vegetation cover: *Pardosa nigriceps*, living on low vegetation (Roberts 1987), and the rare *Arctosa fulvolineata* that inhabits the heterogeneous litter of some salt-marsh habitats (Pétillon et al. 2005a). The vegetation of the natural salt marshes sampled was characterized by a closed canopy of perennial vegetation, in contrast to the vegetation of the restored sites that had a mosaic of bare ground, annual, and perennial plants (Garbutt & Wolters 2008). Such differences may also explain that some halophilic species from young and open successional stages (e.g., *Erigone longipalpis* and *Oedothorax spp.*) were not found in natural salt marshes. In the restored sites, greater species richness would

Table 2.—Species richness, number of individuals, and abundances (number of individuals/day/meter) of the main species (more than 5 individuals) by pitfall traps. Mean parameters are compared between restored and natural habitats by GLM (Whole model: $df = 54$).

Source	Whole model		Site		Habitat		Habitat*Site	
Dependant variable	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species richness	20.86	**<0.001**	25.98	**<0.001**	16.29	**<0.001**	18.02	**<0.001**
Number of individuals	37.56	**<0.001**	35.62	**<0.001**	32.67	**<0.001**	41.95	**<0.001**
Abundance of :								
Oedothorax apicatus	39.35	**<0.001**	39.35	**<0.001**	39.35	**<0.001**	39.35	**<0.001**
Oedothorax fuscus	20.91	**<0.001**	21.45	**<0.001**	22.36	**<0.001**	19.63	**<0.001**
Pardosa prativaga	0.98	0.436	0.84	0.437	1.08	0.303	1.08	0.347
Pardosa purbeckensis	19.68	**<0.001**	17.71	**<0.001**	18.14	**<0.001**	22.41	**<0.001**
Pirata piraticus	3.85	**0.005**	6.61	**0.003**	2.18	0.146	1.94	0.153
Tenuiphantes tenuis	1.34	0.261	2.62	0.082	1.47	0.230	0.00	1.000

then be related to a greater spatial heterogeneity. In the case of young successional stages with uniform habitat (e.g., intensively grazed salt marshes), a general decrease in both plant (Kleyer et al. 2003) and arthropod diversity (Pétillon et al. 2007) are observed, supporting the hypothesis that spider species richness is more determined by habitat structure than by habitat age alone. Also, as web-building species richness is expected to increase with vegetation height (Greenstone 1984), this parameter should be higher in natural habitats than in restored ones. That hypothesis will soon be tested by using data from sweep-net and vortis samplings.

Determinants of species succession in salt marshes.—The second hypothesis of differences in spider populations between natural and restored sites was proven to be valid, especially with the dominance of *Pardosa purbeckensis* in newly created salt marshes. Dominance by a single wolf spider species at the beginning of ecological succession has also been described after fire (*Pardosa saltans* Töpfer-Hofmann 2000 in an Alpine

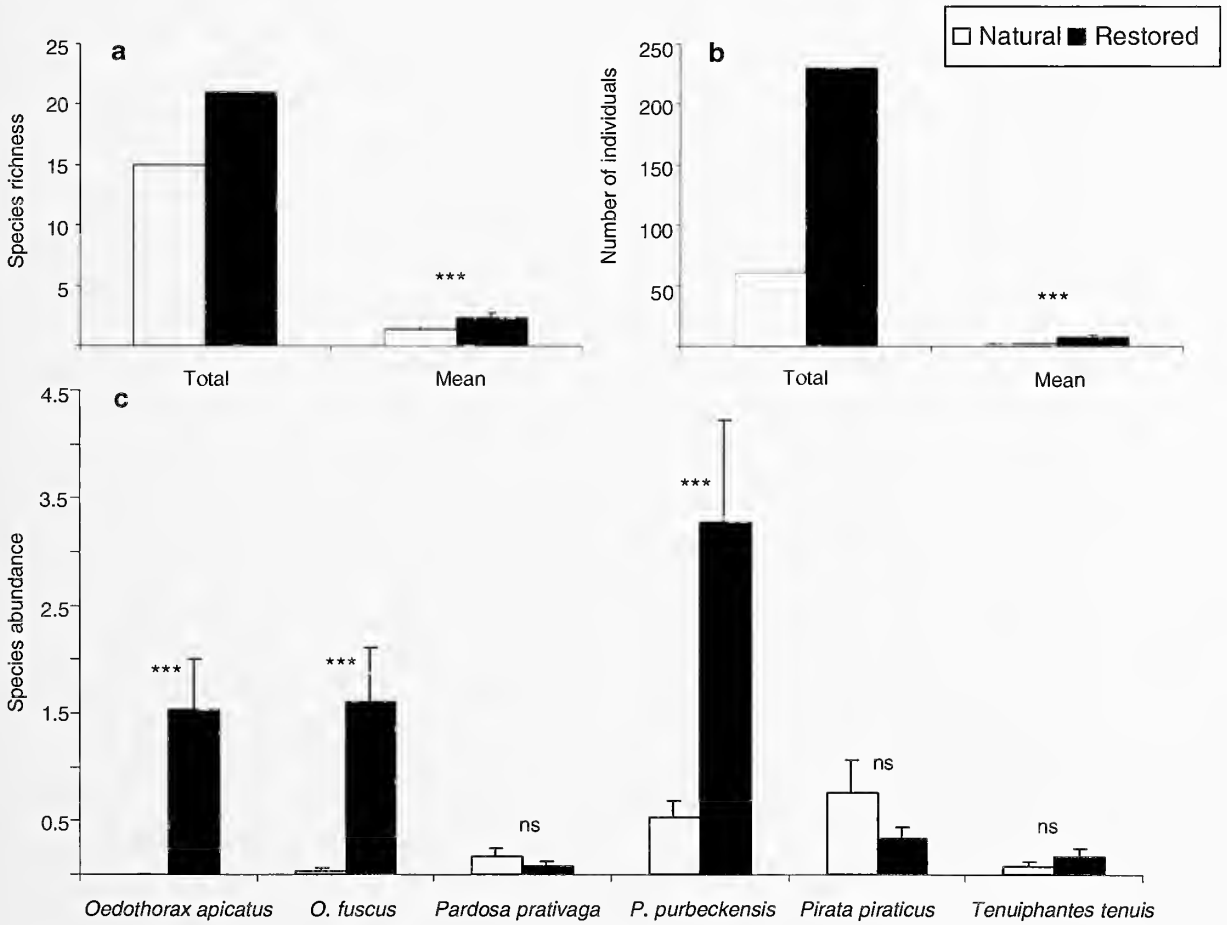

Figure 2.—Total and mean (+ 1 SE, $n = 30$) species richness (a), number of individuals (b) and species abundance (number of individuals/day/meter) (c) in natural and restored salt-marsh habitats. * and ** indicate significant differences by GLM ($P < 0.05$ and $P < 0.01$, respectively; for details on model results, see Table 2).

deciduous forest: Moretti et al. 2002; *Xerolycosa nemoralis* (Westring 1861) in a Finish pine forest: Koponen 2004, 2005). In salt marshes, management practices leading to younger successional stages (like sheep grazing and mowing) are known to favor some halophilic species of high interest (Zulka et al. 1997; Harvey et al. 2002; Pétillon et al. 2007) by opening soil and vegetation structures. Hurd & Fagan (1992) suggested that competition for prey is more important in early successional communities as prey is the limiting resource. Interspecific competition (and mainly intraguild predation) may explain the decrease of some species in late successional stages (Pétillon et al. 2005b). In this study, the comparison between restored and natural habitats showed an important shift in species dominance from *Pardosa purbeckensis* to *Pirata piraticus*. Such a co-existence of these two lycosids has already been reported from German salt marshes (e.g., Heydemann 1961) but does not seem to occur in France (Pétillon et al. 2006). That poses the question of interactions of ground-living spiders in these structurally simple ecosystems (Marshall & Rypstra 1999), depending on successional stages. There is thus a high interest in studying competition and predation between *P. purbeckensis* and *P. piraticus* in different salt-marsh habitats because previous studies have shown differences in the interactions between both species: null (Shaefer 1974), negative for *P. purbeckensis* (Wise 1993) and positive for *P. purbeckeusis* (Pétillon pers.obs.).

Synthesis and perspectives.—The natural salt marshes were characterized by a relatively low species richness, the dominance of late-successional stage species such as *Pirata piraticus*, and the exclusive presence of large species preferring a closed vegetation canopy like *Arctosa fulvolineata* and *Pardosa nigriceps*. Restored habitats were characterized by greater species richness than the adjoining reference habitats, at least during the first years of succession. This is probably due to a more heterogeneous habitat, favoring pioneer species (mainly linyphiids). Restored habitats were also suitable for some halophilic species, in terms of both presence (*Enoplognatha mordax* and *Erigone longipalpis*) and greater abundance (*Pardosa purbeckensis*). Although these results need to be confirmed by a long-term survey, they argue for maintaining a maximum of successional stages in salt marshes as they increase the diversity of halophilic spiders.

Some ecological points need to be studied in more detail. Salt-marsh plants have been found to be effective in colonizing managed realignment sites, albeit predominantly over short distances from the local species pool (Wolters et al. 2005b). In contrast, dispersal has proved to be a critical element of arthropod patterns (e.g., Den Boer 1970). Habitat isolation and size, as well as the fauna of the surrounding habitats (Meijer 1980), could then influence habitat colonization by spiders, leading to different successional patterns in species richness between plants and arthropods. As shown by significant interactions between sites and habitats, this study needs to be completed by studying more specifically the influence of time on restoration success (by considering separately young succesional stages) and the influence of colonization process (i.e., relationships between local, regional species pool and dispersal means, especially for poor-disperser and rare species such as *Arctosa fulvolineata*).

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The value of primary, secondary, and plantation forests for Neotropical epigeic arachnids

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Abstract. Plantations and secondary forests are becoming dominant components of many tropical forest landscapes. Yet we have an insufficient understanding of the value of these habitats for biodiversity conservation, and almost none for most arthropods in species-rich tropical forests. We sampled epigeic arachnids (Amblypygi, Araneae, Opiliones, Scorpiones, and Uropygi) in primary, secondary (14–19 years), and *Eucalyptus* plantation (4–5 years) forests in the Jari region of northeastern Brazilian Amazonia. We sampled five independent sites in each forest type between January and June 2005, collecting a total of 4824 individuals (3177 adults, 112 species), including 1864 adults (75 species) in *Eucalyptus*, 776 (60) in secondary forest, and 536 (72) in primary forest. We compared species richness, species-abundance distributions, and community structure, between the three forest types and identified the species that were characteristic of each forest type. Rarefaction analyses showed that undisturbed primary forest harbored significantly more species and a similar overall abundance as second-growth forest; while levels of species richness were similar between secondary forest and *Eucalyptus*. The species composition and abundance structure of arachnid assemblages was distinct in all three forest types. Considering all species sampled, 19% were only sampled in primary forest, 4% in secondary forest, and 19% in *Eucalyptus*. Most species sampled in plantation forests are known to be wide-ranging habitat generalists. Our data indicate that regenerating forests are not biological deserts (57% and 56% of species sampled in primary forest were also captured in secondary and plantation forests respectively) and can, therefore, help mitigate some of the negative effects of deforestation for epigeic arachnids. However, these replacement habitats do not provide a substitute for primary forest and may fail to conserve many of those species most at risk from extinction.

Keywords: Araneae, Opiliones, Scorpiones, tropical forests, biodiversity, deforestation

The rapid rate of forest conversion in the tropics (FAO 2006) is expected to lead to a massive extinction of tropical forest species (Pimm & Askins 1995; Pimm & Raven 2000). However, the loss of intact forest is being partially offset by the growth of regenerating and planted forests, which are becoming increasingly common across the tropical forest biome (Wright 2005; Grainger 2008), leading to suggestions that the predicted loss of species might be premature (Wright & Muller-Landau 2006). However, these claims are controversial and have been hotly contested due to the lack of empirical evidence that demonstrates the ability of these replacement forests to support native forest species (Gardner et al. 2007a; Laurance 2007), thereby highlighting the importance of research to determine the potential contribution of tropical secondary and planted forests for biodiversity conservation.

At present the conservation value of secondary forests and different plantation forests, from exotic monocultures to mixed-native species stands, remains poorly understood (Freitas et al. 2002; Reid & Huq 2005; Gardner et al. 2007a). Existing studies are few, and often present contradictory conclusions regarding patterns of conservation value depending on the particular taxon sampled and research methods used (Barlow et al. 2007a, 2007c, 2007d; Gardner et al. 2007a, 2007b). Part of the explanation behind the lack of consensus in these studies is the ubiquity of various methodological shortcomings and differences in analytical approach (Gardner et al. 2007a). Typical limitations of studies concerned with the effect of habitat change on tropical forest species include the lack of an undisturbed baseline, non-independence among samples due to limitations in the spatial extent of the study, poor sample representation through low capture or trapping success, and inappropriate analyses (Gardner et al. 2007a). Furthermore, studies of habitat change and tropical forest biodiversity have largely been biased towards birds and terrestrial vertebrates and our understanding of cross-taxon variability in response patterns is embryonic (Barlow et al. 2007a).

We attempted to address the problems outlined above by making a comprehensive and robust evaluation of the value of primary, secondary, and plantation forests for a Neotropical epigeic arachnid fauna (encompassing the orders Amblypygi, Araneae, Opiliones, Scorpiones, and Uropygi). The Brazilian Amazon is a priority area for research on the effects of land-use change on arachnids because the absolute rate of deforestation is among the highest recorded anywhere in the world (Fearnside 2005). Our understanding of the diverse Amazonian arachnid fauna is largely restricted to a small number of well-studied areas of relatively pristine habitat (Heyer et al. 1999), and knowledge of many groups is limited to higher taxa (Adis 2002). Secondary forests are an increasingly dominant feature of the Amazon, following the rapid abandonment of large areas of land in the wake of deforestation (Houghton et al. 2000). In addition a large expansion in the plantation-forest estate is predicted during the coming decades in response to the burgeoning global demand for timber (FAO 2006), with much of the increase expected to occur in Brazilian Amazonia (Fearnside 1998).

By sampling a landscape created by a large-scale forestry project, we minimized the confounding influence of edge

effects and habitat fragmentation and maximized the spatial independence among sites of each forest type. To evaluate the biodiversity consequences of clearing areas of native forest for tree plantations and the potential for faunal recovery through natural regeneration, we examined patterns of alpha and beta diversity for leaf-litter arachnids among the three forest types and compared species-abundance distributions and patterns of assemblage structure and characteristic species in each forest. To our knowledge this is the first ecological study of the value of planted and regenerating forests for arachnids in the neotropics.

METHODS

Study area and site selection.—Sampling was conducted within the Jari Celulose/Grupo Orsa, a 1.7 Mha landholding on the Jari River between the states of Pará and Amapá in north-eastern Brazilian Amazonia (00°27′00″–01°30′00″S, 51°40′00″–53°20′00″W). Sampling was conducted only in the state of Pará. At the time of sampling the landholding was characterized by 53,000 ha of *Eucalyptus* plantations and 50,000 ha of regenerating native vegetation. Fifteen transects were established, with five replicate sites in each of primary, secondary and plantation forests (see either Barlow et al. 2007c or Gardner et al. 2007b for a map). The scale of the landscape enabled us to select study sites that minimized edge effects (the average size of *Eucalyptus* and secondary forest blocks are 17 km^2 and 27 km^2, respectively) and that were spatially independent (average distances between replicate sites within primary, secondary and *Eucalyptus* were 30 km, 9 km, and 11 km respectively). *Eucalyptus* and secondary forest sites were located at similar distances from the nearest areas of continuous primary forest (average distances were 1.1 km and 1.3 km, respectively). The areas of plantation and fallow land we studied were embedded in a large and virtually undisturbed primary forest matrix (> 5000 km^2).

Primary forest sites are dominated by Burseraceae, Sapotaceae, Lecythidaceae, Mimosaceae, and Lauraceae, and are characterized by low levels of anthropogenic influence. The areas of secondary and plantation forest were first cleared (through cutting and burning) between 1970 and 1980. The secondary forest sites are all between 14–19 years of age and are characterized by an abundance of palms, *Inga* spp. and other pioneers. The *Eucalyptus* plantations were sampled between ages 4–5, and are characterized by an understory of annual plants (including many Asteraceae, Rubiaceae, Piperaceae, Poaceae, and Cyperaceae), lianas (e.g., *Davilla* spp., Dilleniaceae) and small trees such as *Vismia* spp. (Clusiaceae), *Mabea taquari*, and *Aparisthmium cordatum* (Euphorbiaceae). Each of the three habitats are distinct with respect to the structure of the canopy, understory and leaf-litter vegetation layers (see Barlow et al. 2007b).

Arachnida sampling.—The arachnids were sampled between January and June 2005 using large dry pitfall traps (35 L buckets, 450 mm deep, with mouth diameter of 350 mm) suitable for sampling a wide range of epigeic organisms including small vertebrates. The buckets were arranged in four-trap arrays, with a 6 m long by 50 cm high plastic drift fence connecting them in a Y-shaped design - composed of one central bucket and one bucket at the end of each arm. Ten consecutive arrays were arranged 100 m apart along each transect. Each sample comprises all arachnids collected over 7 consecutive days in one pitfall array. To minimize loss of specimens to predation and degradation inside the buckets, each array was inspected daily, and all arachnids removed. A total of 50 arrays were sampled over a 14 day period (2 × 7 day samples) in each forest type, producing a total of 100 samples per forest type, and 300 samples in total. Sampling was always conducted across three sites simultaneously, and in nearly every case we sampled sites from different forest types in each sampling session. Consequently the sampling in any given forest type (pooling across all sites) encompassed a wide range of environmental conditions.

All the analyses are based only on adult arachnids. Voucher specimens are stored in the collection of Museu Paraense Emílio Goeldi (MPEG) in Belém, Pará, Brazil. Identification was made using the MPEG reference collection and identification keys (see Adis 2002). Furthermore, some arachnids were identified by specialists at Universidade de São Paulo (Opiliones) and Instituto Butantan (some true spider families and Scorpiones) both in São Paulo, Brazil. A morphospecies number was used when the specific names were unknown (75% of the total number of species, with 56% being identified to the genus level).

Data analysis.—Patterns of species richness between forest types were analyzed by visual inspection of the 95% confidence intervals of individual-based rarefaction curves (EstimateS v.7.5, Colwell 2005). Standardized species-abundance "Whittaker" plots were used to compare species-abundance patterns between different forest types and species assemblages. Non-metric multidimensional scaling (NMDS) was used to define the overall differences in assemblage structure and composition within and among forest types. Ordinations were undertaken for both quantitative (abundance based using square-root transformed site-standardized data and the Bray-Curtis index) and qualitative (presence absence based, Sørenson index) data. We used the similarity percentage (SIMPER) analysis of Clarke & Warwick (2001) to determine the contribution that individual species made toward distinguishing differences in quantitative assemblage structure among forest types. Multivariate analyses were implemented in Primer v.5.

RESULTS

A total of 4824 individuals (3177 adults, 112 species including morphospecies) were collected, including 536 adults (72 species) in primary forest, 777 (60) in secondary forest, and 1864 (75) in *Eucalyptus* plantations. True spiders (Araneae) comprised the majority of the total arachnid fauna constituting 1939 adults (84 species). We sampled more than 71% of the expected number of species in each of the three forest types (Table 1), suggesting that our comparisons of species richness among the three forest types are valid. Sixty-four per cent of all species were recorded in primary forest, and 19% of all species were unique to this habitat (Fig. 1). The same proportion (19%) of the total number of species was also unique to *Eucalyptus* plantations (Fig. 1). By contrast few species (4%) were only found in secondary forest samples. Among the species collected in primary forest, 25% were rare (singletons and doubletons), while in secondary forest and plantations 5% and 20% respectively were rare by this classification.

Table 1.—Speeies richness, and sample completeness for arachnids sampled in primary, secondary and plantation forests in Jari region, Brazil. [a]Number of individuals captured; [b]Number of species observed; [c]Number of species observed as a percentage of the estimated total richness (averaged from 3 estimators, Chao 1, Jack 1 and ACE, Colwell 2005); [d]Percentage of exclusive species sampled (i.e., not sampled elsewhere); [e]Number of species observed as a percentage of the landscape total (all forest types) per site and per forest type.

Forest type	Site	N[a]	Sobs[b]	Coverage[c]	% Exclusive species[d]	Completeness[e]
Primary	Bituba	113	32	77.0	1.8	28.6
	Castanhal	100	28	71.6	1.8	25.0
	Estacao	70	26	60.9	5.4	23.2
	Pacanari	123	33	61.7	1.8	29.5
	Quaruba	130	34	72.2	3.6	30.4
	All	536	72	71.2	18.8	64.3
Secondary	Area 55	78	20	62.8	0.9	17.9
	Area 56	160	30	69.0	0.0	26.8
	Area 75	362	37	75.9	0.9	33.0
	Area 86	43	21	75.2	0.9	18.8
	Area 91	134	17	60.3	0.0	15.2
	All	777	60	81.1	4.4	53.6
Eucalyptus	Area 10	372	32	57.9	3.6	28.6
	Area 127	229	35	47.0	4.5	31.3
	Area 14	766	36	62.5	0.9	32.1
	Area 52	292	21	77.8	0.9	18.8
	Area 95	205	35	57.2	2.7	31.3
	All	1864	75	71.6	18.8	67.0
All Data		3177	112			

Undisturbed primary forest harbored significantly more species of Arachnida than either secondary forest or *Eucalyptus* plantations, although none of the accumulation curves are close to being saturated (Fig. 2). Following the rank abundance analyses, the species-abundance distributions are similar in each forest type (Fig. 3A). Furthermore, the rank-order of species abundances in primary and secondary forest is similar, whereas the species that are superabundant in *Eucalyptus* plantations are either very rare, or not found, in either primary or secondary forests (Fig. 3B). Differences in assemblage structure among habitats were significant for all species assemblages whether they were based on quantitative (ANOSIM, $R = 0.59$, $P < 0.001$, Fig. 4) or qualitative data (ANOSIM, $R = 0.46$, $P < 0.001$). Furthermore, pairwise comparisons revealed that each of the forest types hosted a distinct arachnid assemblage (Fig. 4, quantitative data – $R > 0.36$, $P < 0.02$). The SIMPER analysis illustrated that most of the observed differences in assemblage structure among forest types cannot be attributed to a small number of species (Table 2). However, many of the same species were revealed as being important in distinguishing the arachnid assemblages that were sampled in individual forest types (e.g., *Ancylometes rufus* and *Ananteris pydanieli,* Table 2).

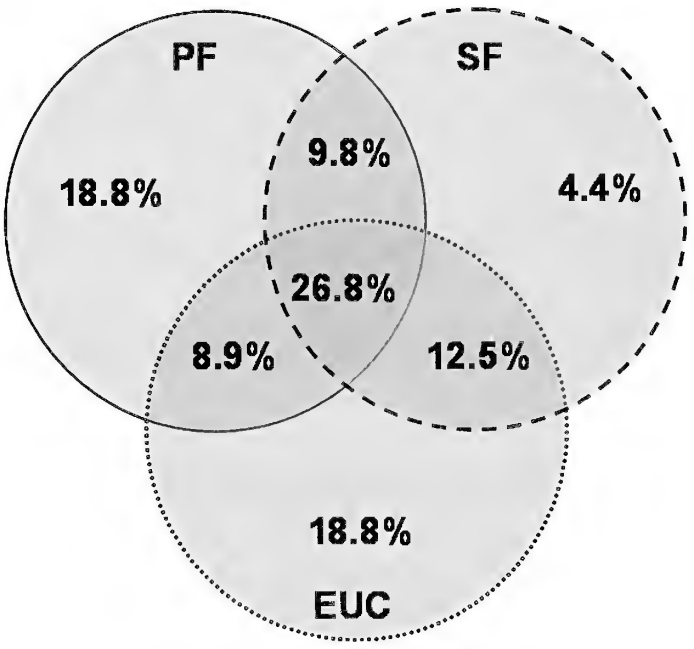

Figure 1.—Venn diagram of all species of arachnid sampled between primary (PF), secondary (SF), and *Eucalyptus* forests (EUC) in our study region.

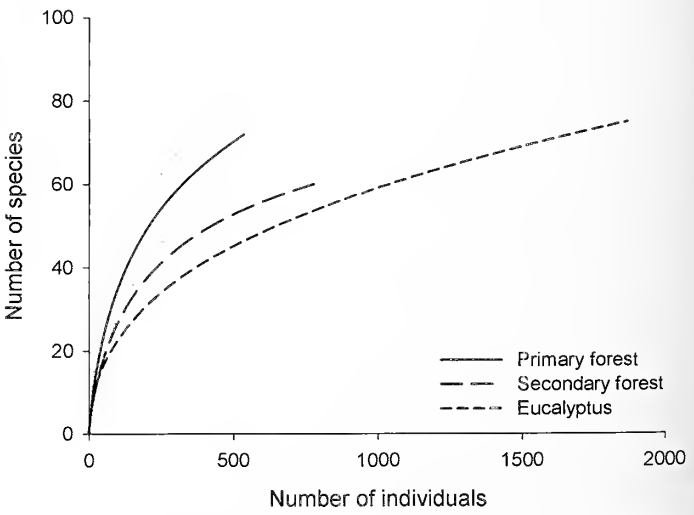

Figure 2.—Individual based rarefaction curves for arachnids in primary, secondary and *Eucalyptus* plantation forests. Fitted dotted lines indicate 95% confidence intervals (shown only for primary forest).

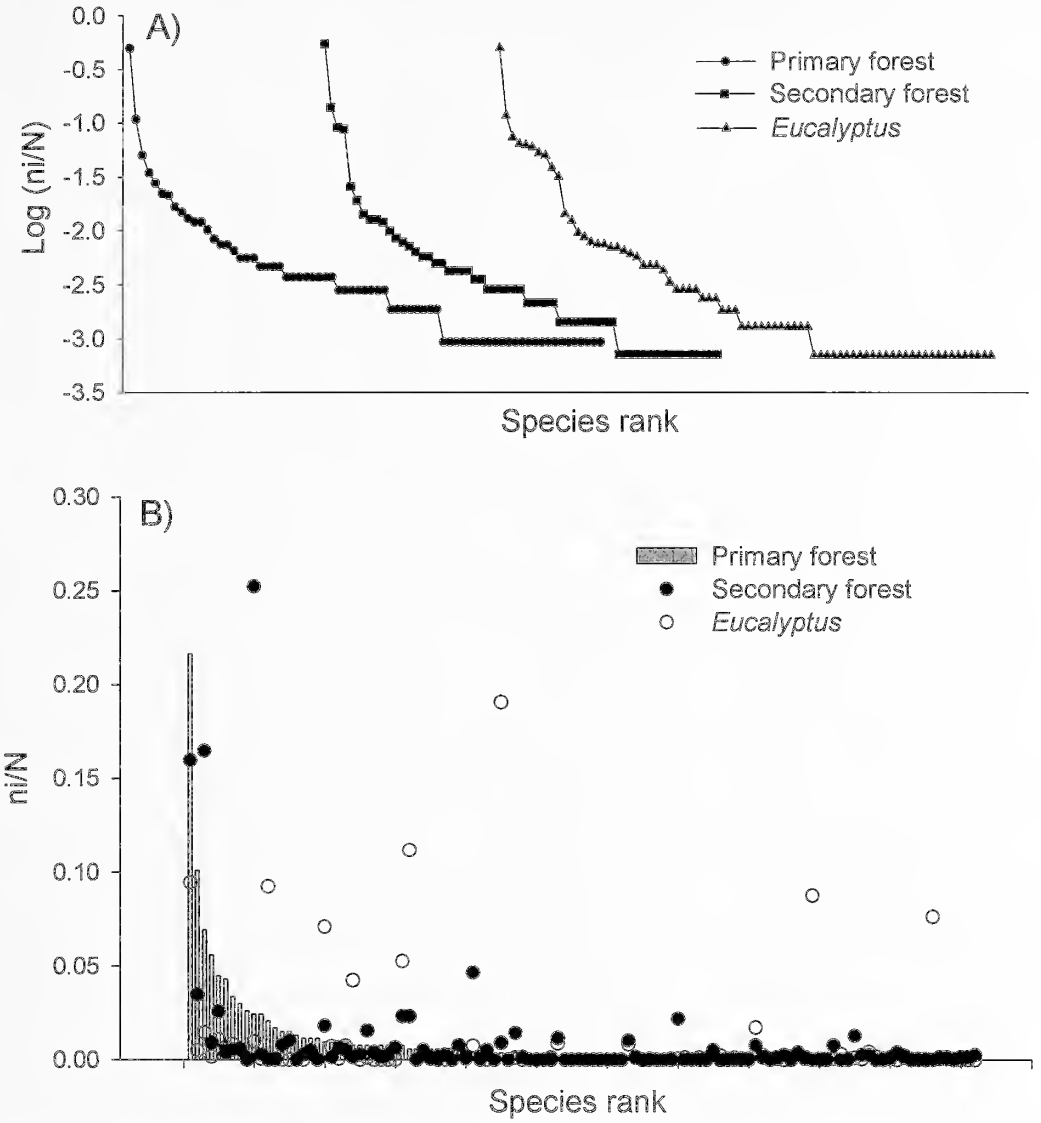

Figure 3.—(A) Dominance diversity (Whittaker) plots for arachnids in primary, secondary and plantation forests of northeastern Brazilian Amazon. Species are ranked according to the number of individuals of each species (ni) and the total of individuals of all species (N) for each forest type. (B) Relative abundance (ni/N) of all species in primary forest. Superimposed are the relative abundances of the same species sampled in secondary forest (filled circles) and *Eucalyptus* plantations (open circles).

DISCUSSION

This study presents the first data comparing patterns of arachnid diversity between primary, secondary, and *Eucalyptus* plantations in the Amazon region. We examine our results with respect to difficulties in the design of biodiversity field studies, patterns of species richness and species composition, and the importance of known environmental associations in explaining species-specific responses to landscape change.

Sampling issues in biodiversity studies.—Understanding the conservation value of human-dominated forest landscapes presents a significant challenge, particularly because of the high cost of biodiversity research (Gardner et al. 2008a) and the lack of investment in taxonomic research (Sheil 2001). This is particularly problematic for arachnids, as the majority of the tropical species are unknown (Redak 2000; Harvey 2002). However the results of many existing biodiversity studies are also confounded because they have been conducted over a small spatial and temporal scale, are vulnerable to edge effects, and often lack independent replication (Gardner et al. 2007a).

We were able to overcome many of the potential methodological problems involved in understanding the conservation value of human-dominated forest landscapes by using a replicated experimental design in large study blocks that minimized edge effects. Even so, our study is not without its own set of problems; 84% of our sample could only be identified to morpho-species (without full Latin binomials), rarefaction curves suggest that our survey was far from complete in any of the habitats and many components of total epigeic arachnid assemblage, especially the small specimens, were not captured by our sampling method (e.g., Oonopidae, Schizomida). There may also be a seasonal bias due to our samples being taken mostly in the wet season, although Adis et al. (1987) did not observe any significant differences in the number of arachnid species captured between the dry and wet seasons in a neotropical secondary forest site.

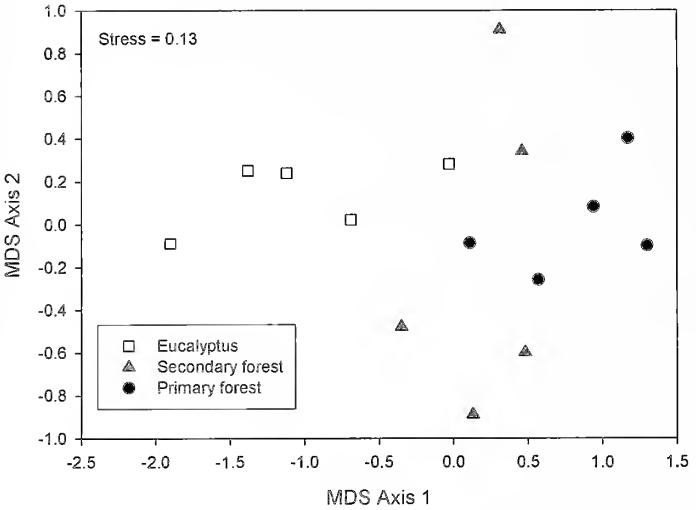

Figure 4.—Multi-Dimensional Scaling (MDS) ordination of arachnid community structure across primary, secondary and *Eucalyptus* forests. Ordination analyses are based on quantitative dissimilarity matrices.

Patterns of species richness.—We found significantly more species of epigeic arachnids in primary forest when compared to secondary forest and *Eucalyptus* plantation, while secondary forest and *Eucalyptus* had similar numbers of species. Barlow et al. (2007a) compared patterns of species richness between epigeic arachnids and 14 other taxa (including other invertebrates, vertebrates and trees) sampled at the same set of study sites and during the same time period. This broad analysis revealed a high level of inter-taxon variability in response patterns to the same gradient of landscape change with individual taxa falling into five major response groups (Barlow et al. 2007a). Epigeic arachnids with significantly more species in primary forest, and no observable difference in species richness between secondary and plantation forests, exhibited the same response pattern as dung beetles (Coleoptera: Scarabaeinae), lizards, and bats (see Gardner et al. 2007b, 2008b).

Patterns of species composition and species turnover.—Despite the fact that each forest type exhibited similar species-abundance distributions, patterns of species composition and community structure were distinct in all three forest types (Fig. 1), matching most other invertebrate and vertebrate taxa sampled at the same sites (Barlow et al. 2007a). Furthermore, these patterns were relatively insensitive to differences in the type of data used (incidence or abundance).

Perhaps surprisingly the same numbers of species were unique to *Eucalyptus* and primary forest sites in our samples (19% of the landscape total in each case), while only five species (4% of total) were caught only in secondary forest. Many of the dominant identified species found in plantation sites can be characterized as wide ranging habitat generalists (e.g., wolf spiders) and are common in open areas (Jocqué & Alderweireldt 2005). The three forest types harbored 30 species that occur in common (27% of total), while 10% and 9% of species were found only in primary and secondary and primary and plantation sites respectively (Fig. 1). These findings were supported by Ferreira & Marques (1998) in the Brazilian Atlantic forest, who show that leaf-litter arthropods sampled in secondary forest more closely reflected primary forest communities than those found in *Eucalyptus* tree monocultures.

The observed dissimilarity in assemblage structure between forest types was only partly driven by differences in abundance of common species (versus differences in species composition) and as such there are few focal species that serve to effectively characterize the different forests in our samples.

Nevertheless, there are some examples where particular forest types are characterized by groups of species, as in the case of the wolf spiders (Lycosidae). It is well known that representatives of Lycosidae are favored by simplified habitats such as grasslands (Jocqué & Alderweireldt 2005) as well as forest areas with shallow leaf litter cover (Uetz 1979). Vegetation structure can have a marked influence on the distribution of arachnid fauna through the provision of suitable microhabitats, including the availability of suitable refuges and appropriate substrata for web attachment (Wise 1993; Indicatti et al. 2005). The fact that representatives of the Lycosidae were absent from both primary and secondary forest samples may indicate that *Eucalyptus* plantations present an appropriately simplified habitat for these species, while it is inaccessible to other species groups.

One particular species that was found only in *Eucalyptus* plantations was the miturgid *Teminius insularis* (Lucas 1857) a widespread species that occurs from Northern Argentina to Florida (Platnick & Ramírez 1991). Although to our knowledge nothing has yet been published on the ecology of this common species, its occurrence in our plantation sites, as well as other anthropogenic environments in Brazilian Amazonia suggests that it represents a true habitat generalist. In contrast, several species which were found to be very common in *Eucalyptus* plantations in this study were previously known from very few specimens elsewhere in Amazonia, and may even represent undescribed species (e.g., *Nops* spp., *Actinopus* spp.). It is possible that these species are opportunists which occupy a niche space (e.g., particular microhabitat) that is rare in primary forest but common in open, disturbed habitat. Marked increases in the abundance of species that are rarely found in native habitat (closed canopy forest) in plantation and secondary forest samples has been observed for many other taxonomic groups (e.g., heliothermic lizards, Gardner et al. 2007b).

A number of recent empirical studies have suggested that secondary forest regeneration can restore conditions suitable for supporting a significant number of primary forest species within decadal time scales (e.g., Dunn 2004; Quintero & Roslin 2005). These positive, yet preliminary results have supported optimistic claims as to the value of secondary forests for the conservation of tropical forest species (Wright & Muller-Landau 2006). Our results partly support this claim in that investment in the conservation of secondary forest may represent an investment in conserving part of the tropical forest biota for our study region (57% and 56% of species sampled in primary forest were also captured in secondary and plantation forests respectively). However, while regenerating forests can mitigate some of the negative effects of deforestation for epigeic arachnids, primary forest represents a seemingly irreplaceable habitat for many species (19% of landscape total in our samples of arachnids) as well as

Table 2.—Pairwise dissimilarities between the different forest types as defined by arachnid assemblages. For each pair of forest types, the top 10 ranked species that contribute to between forest type differences in assemblage structure are listed together with the average abundance in each of the two habitats, the ratio of the average dissimilarity between the two habitats to its standard deviation, and the contribution of that species to the overall observed dissimilarity between the two habitats. Primary (PF); Secondary (SF) and *Eucalyptus* forests (EUC).

	Total dissimilarities 60.9%			
PF-SF	SF	PF	Diss/SD	Contrib%
Ancylometes rufus (Walckenaer 1837)	25.6	7.4	1.11	4.12
Cosmetidae sp. 1	39.2	2.6	1.03	3.91
Ctenidae sp. n. 3	5.4	10.8	1.9	2.97
Ctenidae sp. n. 2	0.6	4.6	1.26	2.77
Broteochactas mapuera Lourenço 1988	1.4	6	1.66	2.74
Fufius sp. 1	7.2	0.4	1.12	2.67
Paratropis sp. 1	0	2.8	1.05	2.43
Hapalopus sp. 1	0.4	2.6	1.49	2.34
Acanthoscurria sp. 2	0.8	3.6	1.26	2.32
Stygnus sp. 1	3.6	0.8	1.08	2.17
Actinopus sp. 1				

	Total dissimilarities 73.9 %			
PF-EUC	EUC	PF	Diss/SD	Contrib%
Nops sp.1	71	0.4	1.96	4.78
Lycosidae sp. 1	32.6	0	1.37	4.35
Ctenidae sp.n. 3	1.8	10.8	2.73	3.64
Teminius insularis (Lucas 1857)	28.4	0	1.02	3.25
Broteochactas mapuera Lourenço 1988	0.6	6	2.45	3.19
Acanthoscurria sp.1	34.4	2.2	1.47	3.11
Ananteris pydanieli Lourenço 1982	26.4	1	1.85	3.08
Ancylometes rufus (Walckenaer 1837)	5.4	7.4	1.35	3.04
Brotheas amazonicus Lourenço 1988	35.2	23.2	1.08	3.03
Stygnus sp. 1	19.6	0.8	1.58	2.6

	Total dissimilarities 67.9 %			
SF-EUC	EUC	SF	Diss/SD	Contrib%
Ancylometes rufus (Walckenaer 1837)	5.4	25.6	1.34	5.96
Lycosidae sp. 1	32.6	0	1.35	5.25
Nops sp.1	71	1.4	1.55	4.59
Acanthoscurria sp. 1	34.4	0	1.68	4.54
Teminius insularis (Lucas 1857)	28.4	0	1.01	3.93
Cosmetidae sp. 1	3.6	39.2	1.02	3.9
Brotheas amazonicus Lourenço 1988	35.2	24.8	1.13	3.76
Abapeba sp. 1	15.8	0.2	2.63	3.22
Actinopus sp. 1	41.6	3.6	0.86	3.02
Ananteris pydanieli Lourenço 1982	26.4	2.8	2	2.94

representing a unique source of colonization for species able to move into degraded habitats (see also Floren & Deeleman-Reinhold 2005).

The results from our study are likely to represent a conservative estimate of the number of species found exclusively in primary forest (both due to taxonomic restrictions and sampling limitations – e.g., we didn't sample in the canopy). Nevertheless, the results presented here, and for other taxa sampled at the same study sites (e.g., dung beetles, Gardner et al. 2008b) suggest a more pessimistic picture of the value of regenerating forest land for native forest species than has been suggested elsewhere (Wright & Muller-Landau 2006). The discrepancy between the results from the Jari landscape and those of studies elsewhere in the tropics is likely to be partly explained by important differences in biogeographical and landscape context, together with the influence of systematic sampling biases. These factors confound our ability to draw general patterns and indicate the danger of understating the tropical forest biodiversity crisis (Laurance 2007). To be effective, management strategies for production landscapes need to emphasize the importance of protecting remaining areas of primary forest. In areas where this is not possible, it is vital that the key methodological and ecological considerations highlighted in our study are given priority when assessing the conservation value of human-dominated forest lands.

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The identity of *Mygale brunnipes* C.L. Koch 1842 (Araneae, Theraphosidae), with a redescription of the species and the description of a new genus

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Abstract. We describe *Kochiana* new genus to accommodate a small Brazilian theraphosine species described originally as *Mygale brunnipes* by Koch (1842), resulting in *Kochiana brunnipes* new combination. Recently, specimens were rediscovered in northeastern Brazilian Atlantic rainforest. A preliminary cladistic analysis using equal weights parsimony and implied weights, was carried out to examine its phylogenetic placement. *Kochiana* new genus was monophyletic in all trees regardless of weighting scheme or concavity used. There is preliminary evidence for *Kochiana* new genus monophyly and weak evidence for its placement as sister group of *Plesiopelma*. *Kochiana* new genus can be characterized by the presence of a hornshaped spermatheca in females and males with a palpal bulb having prolateral accessory keels and a well developed medial crest on the embolus apex.

Keywords: Taxonomy, Avicylariinae, *Eurypelma*, cladistic analysis, Brazilian Atlantic rainforest

The family Theraphosidae so far contains 906 species (Platnick 2008). Approximately 178 species are described from Brazil (Platnick 2008). The taxonomy of the group is complex and revisionary work is needed for most genera. The result is that several species described mainly in the 19th century cannot be identified. The lack of available specimens adds to the taxonomic confusion. Most of them were collected in expeditions carried out by naturalists more than a century ago and most have not been collected again.

The genus *Avicularia* Lamarck 1818 is a typical case. There are 29 *Avicularia* species described in the 19th century that have never been studied after their description, and all are presently considered *nomina dubia* (Platnick 2008). Twenty eight of these *nomina dubia* species were described as *Mygale* Latreille 1802. One of these species is *Avicularia brunnipes* (Koch 1842). It was described as *Mygale brunnipes* by C.L. Koch (1842) and transferred to *Eurypelma* by the same author in 1850 when he erected the genus. When Koch described *Eurypelma*, he did not designate any type species; however, the first one listed in his work, which is usually taken as the type species (Raven 1985), was *Aranea avicularia* Linnaeus 1758, the type species of the genus *Avicularia* Lamarck 1818. Thus, Raven (1985) considered *Eurypelma* a junior synonym of *Avicularia* Lamarck 1818, and the species *M. brunnipes* was subsequently placed in *Avicularia*. Recent collections made by the authors in Northeastern Brazil in conjunction with the rediscovery of the holotype make it possible to redescribe the species and a new genus is erected to accommodate it.

METHODS

Abbreviations: ALE = anterior lateral eyes, AME = anterior median eyes, ap = apical, p = prolateral, PLE = posterior lateral eyes, PME = posterior median eyes, PMS = posterior median spinnerets, PS = prolateral superior keel, r = retrolateral, STC = superior tarsal claws, v = ventral.

Material of the following institutions were examined: ICN = Instituto de Ciencias Naturales, Bogota; IBSP = Instituto Butantan, São Paulo; FCE = Facultad de Ciencias, Entomología, Montevideo; MNRJ = Museu Nacional do Rio de Janeiro, Rio de Janeiro; MNHN = Muséum National d'Histoire Naturelle, Paris; MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo; RWC = Rick C. West private collection, Victoria, British Columbia, Canada; SMF = Senckenberg Museum, Frankfurt; and ZMB = Museum für Naturkunde, Berlin (through photographs).

The measurements are in millimeters. A Nikon SMZ1500 dissecting microscope was used for illustrations (with a *camera lucida* attachment). Male palpal bulb terminology follows Bertani (2000) and spination follows Petrunkevitch (1925) with modifications proposed by Bertani (2001).

Taxa: Outgroups - species of the new genus lack type I urticating hairs, a synapomorphy for a large theraphosine clade (Pérez-Miles et al. 1996). Thus, the outgroups were sampled from outside that large clade from the "basal theraphosine" taxa in the work of Pérez-Miles et al. (1996) and Fukushima et al. (2005). We included representatives of the genera *Chromatopelma* Schmidt 1995, *Cyriocosmus* Simon 1903, *Euathlus* Ausserer 1875, *Grammostola* Simon 1892, *Hapalopus* Ausserer 1875, *Homoeomma* Ausserer 1871, *Maraca* Pérez-Miles 2006 (formerly *Iracema*), *Melloleitaoina* Gerschman & Schiapelli 1960, *Paraphysa* Simon 1892, *Plesiopelma* Pocock 1901, and *Tmesiphantes* Simon 1892. The type species of these genera were included when possible; however, representatives of the type species of *Euathlus*, *Grammostola*, *Melloleitaoina*, *Maraca*, and *Paraphysa* were unavailable. *Melloleitaoina crassifemur* Gerschman & Schia-

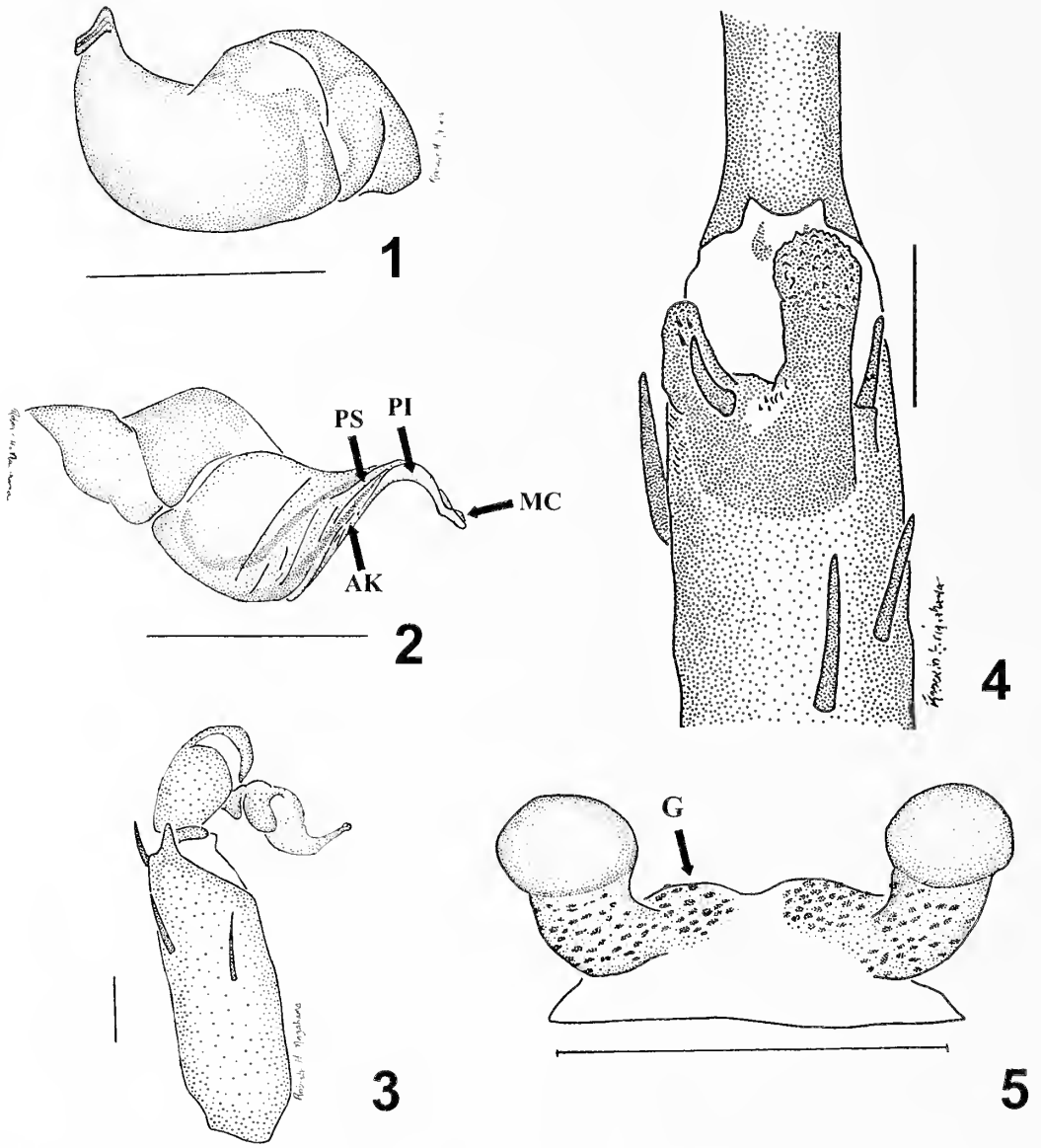
Table 1.—Data matrix showing the distribution of character states used in the cladistic analysis. (? = unknown, - = non-applicable, both treated as missing data in the cladistic analysis).

Taxa/character	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*
Euathlus vulpinus	0	-	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0
Grammostola actaeon	0	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Homoeomma montanum	0	-	0	0	0	1	1	1	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Homoeomma stradlingi	0	-	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maraca horrida	0	-	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Melloleitaoina crassifemur	0	-	0	0	0	1	1	1	0	0	0	0	0	?	0	?	0	0	0	1	0	1	0
Tmesiphantes nubilus	0	-	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Hapalopus formosus	?	?	0	0	0	0	2	0	0	-	0	1	1	0	0	0	0	0	1	0	0	0	1
Hapalopus sp.	0	-	1	0	0	0	2	0	0	-	0	0	1	0	0	0	0	1	1	0	0	0	1
Chromatopelma cyaneopubescens	0	-	0	0	0	0	0	0	0	-	0	1	1	0	0	0	1	0	0	2	0	0	1
Cyriocosmus elegans	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	1
Cyriocosmus nogueiranetoi	1	1	0	0	0	0	0	1	0	3	1	0	0	1	0	0	0	1	0	0	0	0	1
Cyriocosmus sellatus	1	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0
Paraphysa scrofa	0	-	0	0	0	0	0	1	0	2	0	0	0	?	0	?	0	0	0	1	0	1	0
Plesiopelma longisternale	0	-	0	1	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0
Plesiopelma insulare	0	-	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Kochiana brunnipes	0	-	0	0	1	1	1	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0
Kochiana sp.	0	-	0	0	1	1	1	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0

pelli 1960 and *Paraphysa scrofa* Molina 1788 data used for cladistic analysis were based on Gerschman & Schiapelli (1960), Schiapelli & Gerschman (1963), and Pérez-Miles et al. (1996). *Chromatopelma* was included due to the resemblance of genitalia with *Hapalopus*, its probable sister group.

Material examined for cladistic analysis: *Chromatopelma cyaneopubescens* (Strand 1907), VENEZUELA: without further information, 1 male SMF 39012, Ockert ded. (female's characters were collected from literature). *Cyriocosmus elegans* Simon 1889, VENEZUELA: without further information, MNHN 9863; TOBAGO ISLAND: *Speyside* (11°18′N, 60°32′W): in road cut ground burrows, 2 males RWC, 19 May 1980. *Cyriocosmus nogueiranetoi* Fukushima et al. 2005, BRAZIL: *Rio Branco* (9°58′S, 67°48′W): female holotype IBSP 9193, D. Pinz col., November 1996 and male paratype IBSP 8899 from same locality and collector. *Cyriocosmus sellatus* (Simon 1889), BRAZIL: *Upper Amazonas*: holotype female MNHN 8102; *Serra do Divisor* (9°08′S, 72°40′W): IBSP 8900, R.M. Vieira et al. col., 05–25 November 1996. *Euathlus vulpinus* (Karsch 1880), CHILE: *Osorno* (40°38′S, 72°19′W): 3 males IBSP 3817B and 1 female IBSP 3817A. *Grammostola actaeon* (Pocock 1903), BRAZIL: *Colônia Ouro Verde*: 1 male IBSP 2124, F. Haas col., 1949; *Monte Verde* (22°51′S, 46°02′W): 1 female IBSP 8725, H. Shiefferclocker col., 19 January 1999. *Hapalopus formosus* Ausserer 1875, COLOMBIA: *Sierra Nevada de Santa Marta*: 1 male ICN-AR 1981 and 1 female ICN-AR 1982, P. Sanchez col., July 2001. *Hapalopus* sp., BRAZIL: *Miracema do Tocantins* (9°34′S, 48°23′W): 1 male ISBP 10752, R. Bertani & V.L. Iost col., 11–21 September 2001 and 1 female IBSP 9749 from same locality and collectors. *Homoeomma montanum* (Mello-Leitão 1923), BRAZIL: *Petrópolis* (22°30′S, 43°10′W): 1 male MNRJ 13771, A.M. Zacelly col., July 1975; *Parque Nacional do Itatiaia* (22°45′S, 44°50′W): MZSP 10893, Luederwaldt col., May 1906; *Lima Duarte* (21°50′S, 43°47′W): Parque Estadual de Ibitipoca, 1 female IBSP 8928, A. de Oliveira & B.M. Souza col., 08 November 1997. *Homeomma stradlingi* O. Pickard-Cambridge 1881, BRAZIL: *Petrópolis* (22°30′S, 43°10′W): CEDEA, Bairro Rocio, 1 male MNRJ 14994, E.C.P. Pombal col., 19 August 2006; *Rio de Janeiro* (22°54′S, 43°12′W): Floresta da Tijuca, 1 female MNRJ 12937, R. Costa col., 06 July 1999. *Maraca horrida* (Schmidt 1994), BRAZIL: *Miracutu*: Parque Nacional do Jaú, 1 male and female IBSP 9377, M.E.E.S. Oliveira col., 1995. *Plesiopelma insulare* (Mello-Leitão 1923) BRAZIL: *Ilha de São Sebastião* (23°46′S, 41°21′W): 1 male MZSP 3138, H. Urban col., August 1963 and 1 female MZSP 14876, H. Urban col., 01 March 1964. *Plesiopelma longisternale* (Schiapelli & Gerschman 1942) URUGUAY: *Maldonado*: Punta Ballena (34°55′S, 55°03′W), 1 male FCE-MY 0424, C.S. Carbonell col., 19 April 1963 and *Maldonado* (34°54′S, 54°56′W): Cerro al NW de Sierra de Animas, 1 female FCE-MY 0491, F. Costa, R. Capocasale, F. Pérez-Miles & E. Gudynas col., March 1989. *Tmesiphantes nubilus* Simon 1892, BRAZIL: *Una* (15°16′S, 39°04′W): Reserva Biológica do Una, 1 male MZSP 28778 and 1 female MZSP 28780, K. Kato col., December 1999. *Kochiana* sp., BRAZIL: *Santa Luzia do Itanhy* (11°21′S, 37°26′W): Crasto, 2 males IBSP 9914 and IBSP 8548 and 2 females IBSP 9347 and IBSP 11439, A.D. Brescovit, R. Bertani, & A.B. Bonaldo col., September 1999. Specimens of this undescribed species of *Kochiana* were examined and characters scored for cladistic analysis *in loco*. However, we were not granted a loan of the specimens for a more careful study and illustration of genitalia, precluding its description here.

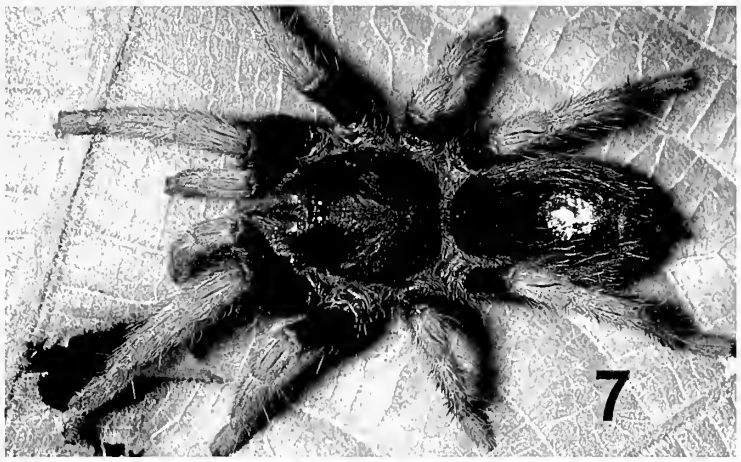
Cladistic analysis was based primarily on the matrix of Fukushima et al. (2005) (characters 0–3, 8, 11, 15–22 from Table I) and some characters were added (4–7, 13 and 23). Character 1 of Fukushima et al. (2005) was here split in two (characters 1 and 2, Table I). The spermathecal characters (except 10, 11, and 14) were modified from Fukushima et al. (2005). Presence of type IV urticating hair was proposed by Pérez-Miles et al. (1996) as a synapomorphy for a group of five theraphosine genera (*Plesiopelma*, *Homoeomma*, *Grammostola* [formerly *Phrixotrichus*], *Cyriocosmus*, and *Para-*

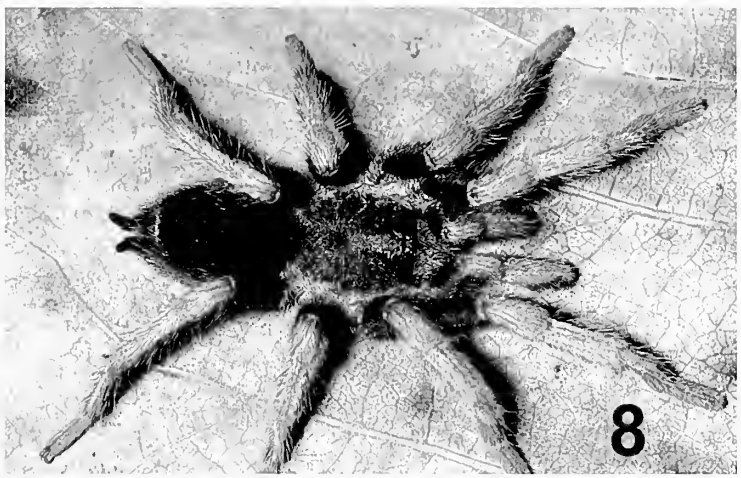


Figures 1–5.—*Kochiana brunnipes* new combination. 1–4. Male (MZSP 28774), left palp; 5. Female (MZSP 28776). 1. Male palpal bulb, retrolateral; 2. Prolateral; 3. Palp, prolateral; 4. Leg I tibial apophysis, ventral; 5. Spermathecae, ventral. Scale bar = 1 mm. AK = accessory keels. MC = medial crest. G = granules. PI = prolateral inferior keel. PS = prolateral superior keel.

physa). The high degree of variation found in the morphology of urticating hairs examined did not allow us to determine satisfactorily the presence or absence of this type of urticating hair. Hence, we did not include this character in the cladistic analysis.

Characters and states as follows: (0) Paraembolic apophysis: absent = 0; present = 1 (see figs. 1–20 Fukushima et al. 2005). (1) Paraembolic apophysis: short (less than a half of embolus length) = 0 (see figs. 1–10 Fukushima et al. 2005); long (more than half of embolus length) = 1 (see figs. 11–20 Fukushima et al. 2005). (2) Prolateral inferior keel: undivided = 0; divided = 1 (see fig. 16 of Bertani 2000). (3) Prolateral inferior keel: without tooth = 0; with tooth = 1 (see fig. 4 of Schiapelli & Gerschman de Pikelin, 1979). (4) Prolateral accessory keels on male palp: absent = 0, present = 1 (Figs. 1, 2). (5) Medial crest on embolus apex: absent or weakly developed = 0, well developed = 1. (6) Embolus position: upward = 0, downward = 1, straight = 2. (7) Embolus: short (less than half of bulb length) = 0, long (more than half of bulb length) = 1. (8) Digitiform basal apophysis in the male palpal bulb: absent = 0; present = 1 (see fig. 25 of Pérez-Miles et al. 1996). (9) Spermathecal neck: straight = 0 (fig. 37 of Pérez-Miles et al. 1996), spiraled = 1 (see figs. 35–39 of Fukushima et al. 2005), horn-shaped = 2 (Fig. 5), twisted = 3 (see fig. 34 of Fukushima et al. 2005). (10) Spermatheca: without convex basal plate = 0; with convex basal plate = 1 (see figs. 34–39 of Fukushima et al. 2005). (11) Number of spermatheca: two = 0; one = 1. (12) Spermatheca: with membranous base weakly developed = 0; with membranous base well developed = 1 (see fig. 54 of Fukushima et al. 2005). (13) Spermatheca: without large granules = 0, with several large granules = 1 (Fig. 5). (14) Spermatheca: without caliciform seminal receptacle = 0, with caliciform seminal receptacle = 1 (see figs. 35–39 of Fukushima et al. 2005). (15) Retrolateral cymbium: without a field of spines = 0, with a field of spines = 1 (Fig. 11). (16) Male retrolateral palpal tibia: without spiniform structures =





Figures 6–8.—*Kochiana brunnipes* new combination. 6. Reproduction of Koch's 1842 original illustration of *Mygale brunnipes*; 7. Female; 8. Male. Both from Murici, state of Alagoas, Brazil. Photos: R. Bertani.

0, with spiniform structures = 1 (Fig. 11). (17) Retrolateral process on the male palpal tibia: absent = 0; present = 1 (Fig. 11). (18) Tibial apophysis of leg I: two divergent branches = 0 (see figs. 27, 28 of Fukushima et al. 2005); two convergent branches = 1 (see fig. 83 of Gerschman de Pikelin & Schiapelli 1973). (19) Flexion of male metatarsus I: between two branches = 0; on the retrolateral side of retrolateral branch = 1, on the apex of the retrolateral branch = 2. (20) Tubercle on male metatarsus I: absent = 0; present = 1 (see fig. 39 of Pérez-Miles et al. 1996). (21) Number of labial cuspules in males: more than 50 euspules = 0, less than 30 cuspules = 1. (22) Dorsal abdominal pattern: without stripes = 0; with stripes = 1 (see figs. 42–48 and 50 of Fukushima et al. 2005).

Table 2.—*Kochiana brunnipes* new combination. Male MZSP 28774 from Murici, state of Alagoas, Brazil. Length of left legs and palpal segments.

	Palp	I	II	III	IV
Tarsi	1.91	3.71	3.50	4.46	4.21
Metatarsi	—	6.29	5.30	5.60	7.78
Tibiae	4.23	5.37	5.51	4.20	6.68
Patellae	3.14	4.35	4.11	3.54	3.88
Femora	5.64	7.70	7.36	6.45	8.37

Computer Methods: A data matrix with 23 characters and 18 taxa was analyzed. Cladistic analysis was carried out using computer programs: Nona 2.0 for Windows (Goloboff 1998) and X-Pee-Wee 1.3 for Windows (Goloboff 1997). For X-Pee-Wee 1.3 and Nona 2.0 the commands h100, h/20, amb- and mult*50 were used. For Pee-Wee the concavities from 1 to 6 were used. Characters were treated as non-additive. Bremer support values were calculated using Nona 2.0 with commands H50000, bsupport3.

TAXONOMY

Family Theraphosidae Thorell 1870

Kochiana new genus

Mygale Latreille 1802:345 (in part: *Mygale brunnipes* C.L. Koch 1842). Type species by original designation *Aranea avicularia* Linnaeus 1758, from Ameriea, no speeific locality, type presumed lost (Raven 1985:146).

Eurypelma C.L. Koch 1850:74 (in part: *Eurypelma brunnipes* (C.L. Koch 1842)). Type species by original designation *Aranea avicularia* Linnaeus 1758, from America, no specific locality, type presumed lost (Raven 1985: 146).

Avicularia Lamarck 1818:107 (in part: *Avicularia brunnipes* (C.L. Koch 1842)). Type species by original designation *Aranea avicularia* Linnaeus 1758, from America, no specific locality, type presumed lost (Raven 1985:146).

Table 3.—*Kochiana brunnipes* new combination. Female MZSP 28776 from Murici, state of Alagoas, Brazil. Length of left legs and palpal segments.

	Palp	I	II	III	IV
Tarsi	2.65	2.42	2.60	2.61	3.38
Metatarsi	—	3.92	3.77	4.43	6.84
Tibiae	3.54	4.77	3.86	3.08	5.39
Patellae	3.24	4.47	3.86	3.40	3.81
Femora	5.18	6.45	5.73	5.26	6.89

Type species.—*Mygale brunnipes* C.L. Koch 1842.

Etymology.—The name is a patronym in honor of C.L. Koch, an important XIX century arachnologist who described this species and many other Brazilian theraphosids.

Diagnosis.—Males of *Kochiana* new genus resemble *Homoeomma*, *Tmesiphantes*, *Melloleitaoina*, *Plesiopelma*, and *Grammostola* by the male palpal bulb having a long and narrow embolus pointing downward. They can be distinguished by having prolateral accessory keels on the palpal bulb (Fig. 2). Additionally, they differ from *Tmesiphantes*, *Melloleitaoina*, and *Grammostola* by the metatarsus I folding between the two branches of the tibial apophysis (Fig. 4); from *Plesiopelma* by lacking the metatarsus tubercle on the male leg I and from *Homoeomma* by not presenting the digital apophysis on the male palpal bulb. Females can be distinguished by the horn-shaped spermathecae with large granules (Fig. 5).

Description.—See description of type species.

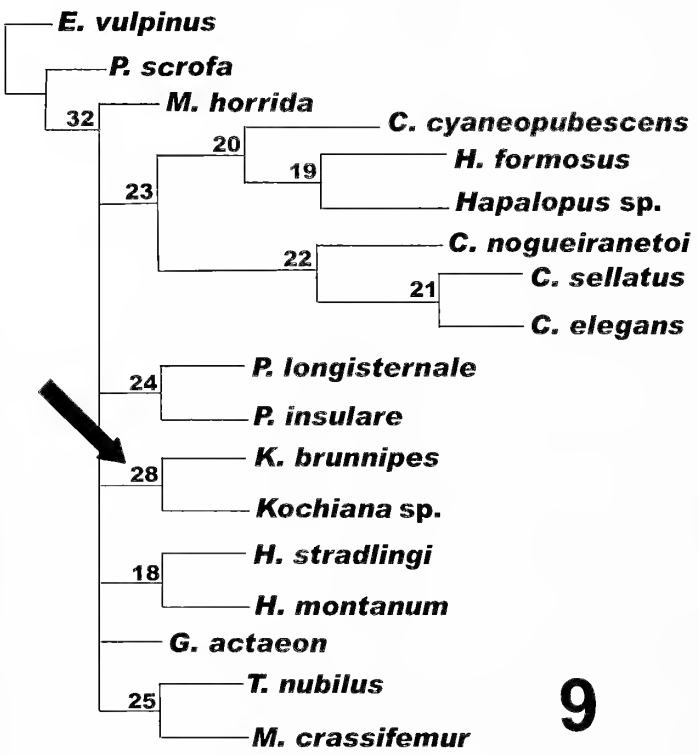


Figure 9.—Strict consensus of eight trees obtained with X-Pee-Wee 1.3 with concavity 6. Fit = 1928.57, length = 40, with clade numbers. *Kochiana* new genus is indicated by an arrow. Synapomorphies of the genus include prolateral accessory keels and well developed medial crest on embolus apex (node 28, Table IV).

Table 4.—Synapomorphies and autapomorphies for the cladogram presented in Fig. 9.

Taxa or Node	Character	Change	Taxa or Node	Character	Change
H. montanum	5	0 → 1	Node 21	14	0 → 1
Hapalopus sp.	2	0 → 1		15	0 → 1
	17	0 → 1		16	0 → 1
C. sellatus	22	1 → 0	Node 22	0	0 → 1
C. elegans	1	1 → 0		10	0 → 1
P. longisternale	16	0 → 1	Node 23	22	0 → 1
C. cyaneopubescens	16	0 → 1	Node 24	3	0 → 1
	19	0 → 2		20	0 → 1
Node 18	8	0 → 1	Node 25	5	0 → 1
Node 19	6	0 → 2	Node 28	4	0 → 1
	18	0 → 1		5	0 → 1
Node 20	7	1 → 0	Node 32	9	2 → 0
	12	0 → 1			

Kochiana brunnipes (C.L. Koch 1842) new combination

Mygale brunnipes C.L. Koch 1842:35, pl. CCXCIX, fig. 713, 1 female holotype from Brazil, Freir. col., ZMB-2071; Petrunkevitch 1911:79 (*nomen dubium*); Roewer 1955: 1595 (*nomen dubium*)

Mygale brunea Simon 1864:68 (misidentification per Bonnet 1957:2992)

Mygale brunneipes Bonnet 1957:2992

Eurypelma brunnipes C.L. Koch 1850:74

Avicularia brunnipes Platnick 2008 (*nomen dubium*)

Figs. 1–8.

Diagnosis.—See diagnosis for the genus.

Table 5.—Character steps and fit of the cladogram presented in Fig. 9.

Character	Fit	Steps	Extra Steps
0	100	1	0
1	—	—	—
2	—	—	—
3	100	1	0
4	100	1	0
5	75	3	2
6	100	2	0
7	100	1	0
8	100	1	0
9	75	5	2
10	100	1	0
11	85.7	2	1
12	100	1	0
13	85.7	2	1
14	100	1	0
15	100	1	0
16	75	3	2
17	75	3	2
18	100	1	0
19	85.7	3	1
20	100	1	0
21	85.7	2	1
22	85.7	2	1

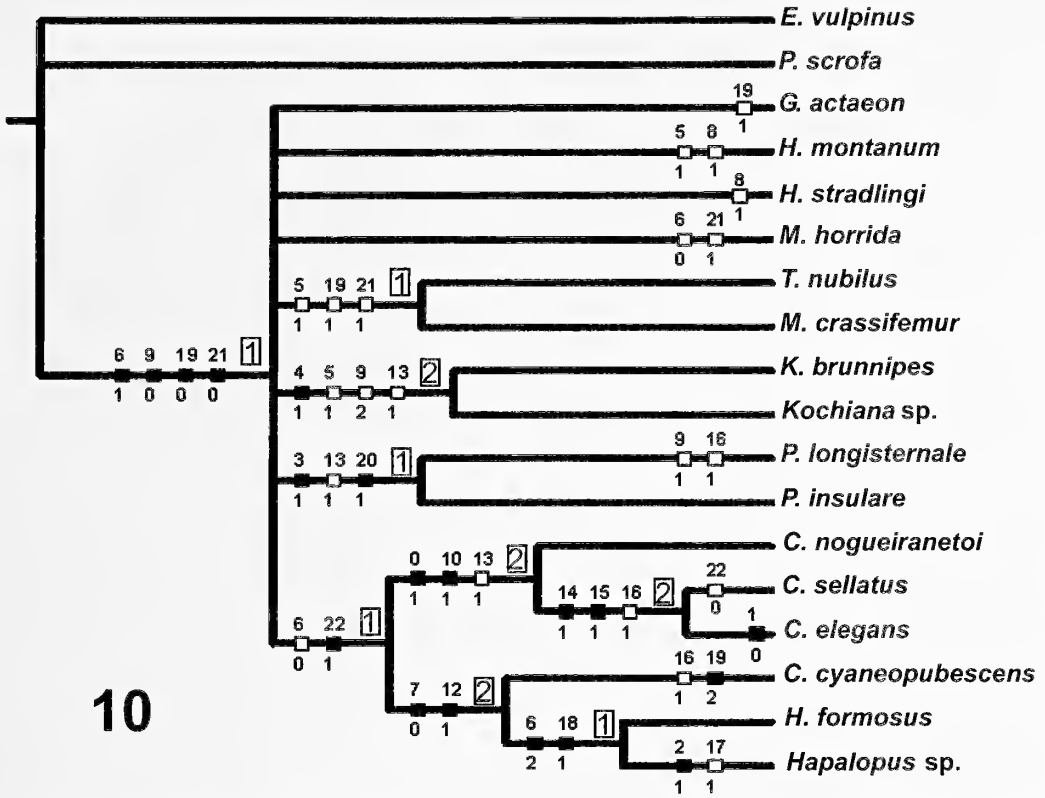


Figure 10.—Striet consensus of 16 trees obtained with Nona 2.0. Length = 46, CI = 58, RI = 65. Character support is shown with white squares indicating homoplastic characters and black squares indicated characters without any homoplasy. Numbers above and under the squares indicating the character and character states, respectively. Bremer support values appear inside a rectangle close to each internode.

Type material.—BRAZIL: holotype female, ZMB-2071 (dry pinned specimen, too fragile to mail, examined by photograph).

Note.—Although the holotype is faded, it retains its original cephalothorax and leg coloration, making it recognizable despite the poor original description. Additionally, the color plate provided by C.L. Koch (Fig. 6) shows the typical color pattern in detail, which agrees in full with the recently collected specimens. Though the author stated the type locality as only "Brazil," many of the Brazilian species described by him came from the Northeastern Coast, the same place where the new specimens were recollected. No other Brazilian theraphosid presents this typical coloration.

Description.—Male, MZSP 28774, BRAZIL: *Alagoas*: Murici, Murici Ecological Station (9°14′S, 35°47′ W), elev. 354 m, R. Bertani, D.M.R. Ortega & R.H. Nagahama, 13 August 2006. Total length, not including chelicerae or spinnerets 24.07. Carapace: length 9.73, width 8.34. Anterior eye row slightly procurved, posterior row recurved. Eyes sizes and interdistances: AME 0.46, ALE 0.48, PME 0.24, PLE 0.38, AME–AME 0.11, AME–ALE 0.13, PME–PME 0.70, PME–PLE 0.11, ALE–PLE 0.08, AME–PME 0.03, ALE–ALE 0.68, PLE–PLE 0.87, AME–PLE 0.36. Eye tubercle: length 1.06, width 1.66, clypeus absent. Fovea: slightly procurved and shallow. Labium: length 1.05, width 0.88, with approximately 82 cuspules. Maxillae: between 100–200 cuspules in the inner corner. Sternum: length 4.83, width 3.89. Sigilla: large 1st pair; small 2nd pair, more than 1.5 diameter from margin; 3rd pair more than two diameters from margin and a larger 4th fusiform pair, more than two diameters from margin. Left chelicera with 11 teeth on promargin and a row of small teeth on promargin. Scopulae present on 2/3 of metatarsi I, on distal half of metatarsi II, 1/3 on III and less than 1/4 distal of metatarsi IV. Tarsi I–IV densely scopulate, scopulae of tarsi III divided by narrow band of setae, tarsi IV widely divided by setae. Length of legs and palp in Table II. Spination on the left legs and palp: palpal femur r0-0-1, tibia p0-2-0; leg I: tibia v1-1-0, p0-1-1, r 1-1-1ap, metatarsus v0-0-2ap; leg II: tibia v2-2-2ap, p0-0-1, metatarsus v1-0-3ap; leg III: tibia v1-1-2ap, p0-1-0, r0-1-1, metatarsus v1-1-3ap, p1-3-1ap, r0-1-0; leg IV: tibia v1-1-2ap, p1-1-0, r0-1-1, metatarsus v2-2-3ap, p0-1-1ap, r0-1-1. Coxae I–IV without stridulatory setae. STC smooth. PLS segment lengths: apical 2.25, medial 1.84 and basal 2.70. PMS rounded and small. Urticating hairs type III. Pilose black cephalothorax; labium, sternum, coxae and femora with blackish pattern; patellae to tarsi reddish light brown. Black abdomen with golden cordiform area on central dorsal region corresponding to the urticating hair patch (Fig. 8). Male palpal bulb with prolateral superior and prolateral inferior keels (Fig. 2). PS well-developed (Fig. 2). Retrolateral and apical keels absent. (Figs. 1, 2). Presence of prolateral accessory keels between the prolateral superior and inferior keels (Fig. 2). Embolus apex with well developed medial crest (Fig. 2). Leg I tibial apophysis two-branched with retrolateral branch longer than prolateral (Fig. 4). Metatarsus I folds between the two branches of the tibial apophysis (Fig. 4).

Female: (MZSP 28776, same data as male). Total length, not including chelicerae or spinnerets 25.18. Cephalotorax length 9.60, width 7.94. Anterior eye row slightly procurved,

posterior row straight. Eyes sizes and interdistances: AME 0.11, ALE 0.44, PME 0.23, PLE 0.44, AME–AME 0.11, AME–ALE 0.14, PME–PME 0.72, PME–PLE 0.07, ALE–PLE 0.05, AME–PME 0.06, ALE–ALE 1.02, PLE–PLE 1.10, AME–PLE 0.41. Eye tubercle length 1.10, width 1.80, clypeus absent. Fovea procurved and shallow. Labium length 1.37, width 1.39 with approximately 97 cuspules. Maxillae: approximately 100 cuspules in the inner corner. Sternum length 4.55, width 3.89. Sigilla: large 1st pair; 2nd and 3rd pair not visible and a larger 4th fusiform pair, one diameter from margin. Left chelicerae with 12 teeth and a row of small teeth on promargin. Tarsi I–IV densely scopulate, scopulae of tarsus II divided by a narrow band of setae, tarsi III–IV widely divided by setae. Metatarsi I–II densely scopulate on distal half, III densely scopulate on 1/3, and IV densely scopulate less than 1/4 region. Length of legs and palp in Table III. Spination of the left legs and palp: palpal tibia v0-2-2ap; leg I: tibia v0-1-2ap, metatarsus v0-1-2ap; leg II: tibia v0-1-2ap, metatarsus v1-1-3ap; leg III: tibia v0-2-2ap, p0-1-1, r0-0-2, metatarsus v2-2-3ap, p1-1-1ap, d0-0-I; leg IV: tibia v0-2-2ap, r0-1-1, metatarsus v1-3-3ap, p0-1-1, r0-1-1ap. Coxae without stridulatory hairs. STC smooth. PLS segment lengths: apical 2.45, medial 1.66 and basal 2.56. PMS rounded and small. Urticating hairs type III. Color pattern as in male (Fig. 7). Two horn-shaped spermathecae with several large granules (Fig. 5).

Additional material examined.—BRAZIL: *Alagoas*: Murici, Murici Ecological Station (9°14′S, 35°47′W), 1 male MZSP 28775, R. Bertani, D.R.M. Ortega & R.H. Nagahama, 12 August 2006; Murici Ecological Station (9°15′S, 35°48′W), 1 female MZSP 28777, R. Bertani, D.R.M. Ortega & R.H. Nagahama, 13 August 2006.

Distribution.—Northeastern Brazil: states of Paraíba and Alagoas, in fragments of Atlantic rainforest.

Note.—Living specimens from State of Paraiba, Areia (7°15′00″S, 36°49′60″W) were collected by A.D. Brescovit, R. Bertani, & A.B. Bonaldo, September 1999.

CLADISTICS

Eight trees were obtained using implied weighting with concavities 3 to 6 in X-Pee-Wee 1.3 (fits 1815.00, 1866.66, 1902.38, 1928.57 respectively for concavities 3, 4, 5, and 6 and length 40 for all of them). In six trees *Kochiana* new genus was a monophyletic group with *Plesiopelma*. In one of the remaining two trees *Kochiana* new genus traded place in a trichotomy with *Plesiopelma* (*Cyrioscosmus* (*C. cyaneopubescens* + *Hapalopus*)) and in the other tree it traded place in a polytomy with all these clades plus *Homoeomma*. Eleven trees (fit = 1600.00, length 41) were found with concavity 1 and ten trees (fit = 1733.33, length 41) with concavity 2. In both *Kochiana* new genus resulted as a monophyletic group with *Plesiopelma* or was collapsed in a trichotomy with *Plesiopelma* and *Cyriocosmus*. Figure 9 shows the consensus of the trees obtained using X-Pee-Wee and concavity 6 (Tables I, IV, and V). It was chosen as the preferred tree due to the higher fit and lower number of steps. The node 28 (Table IV) on Fig. 9 referred to the synapomorphies of *Kochiana* new genus: presence of accessory keels (character 4 in Tables I and V) and medial crest (character 5 in Tables I and V) on male palpal bulb.

Figure 11.—Retrolateral right palpal tibia of male *Cyriocosmus elegans* (RWC). Black arrow pointing to a field of spines on cymbium; white arrow pointing to a field of spiniform hairs on tibia; grey arrow pointing to a process on tibia. Scale bar = 1 mm. Photo: R. Bertani.

Using Nona 2.0 with equal weighting and the same commands used above produced 16 trees (length = 40, ci = 67, ri = 76). The eight trees found by X-Pee-wee were also found by Nona. The other eight trees differed in the position of *H. montanum*, which appeared as a sister group of *Kochiana* new genus. The consensus tree (length = 46, ci = 58, ri = 65) of 16 trees obtained with Nona is shown in Figure 10. *Kochiana* synapomorphies include accessory keels on male palpal bulb (character 4 in Table I), and putatively a medial crest on embolus apex (character 5 in Table I), horn-shaped spermatheca (character 9 in Table I) and spermatheca with large granules (character 13 in Table I) (Fig. 10). Bremer support values are also shown in Fig. 10. The Nona consensus (Fig. 10) differed from the X-Pee-Wee consensus (Fig. 9) only by collapsing *H. montanum* and *H. stradlingi*.

Kochiana new genus was monophyletic in all analyses regardless of weighting scheme or concavity used. Thus, there is preliminary evidence for *Kochiana* monophyly and weak

evidence for its placement as sister to *Plesiopelma*. A more detailed analysis including representatives of all theraphosine genera is necessary to confirm the placement of *Kochiana* new genus.

As for *Kochiana brunnipes* new combination, many species described during the 19th century await "rediscovery" by modern taxonomists. As such taxa remain overlooked, they are not compared with the recently collected specimens and are not considered when new species are being described. This may result in the creation of junior synonyms and thus add to the taxonomic chaos. The study of these neglected species may aid in solving these problems and improving the taxonomy of theraphosids.

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Allozyme characterization of *Hogna* species (Araneae, Lycosidae) of the Galápagos Archipelago

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Abstract. The colonization of species on remote islands may result in phenotypic diversification and ultimately speciation. On the Galápagos Archipelago, seven very closely related morpho-species of the wolf spiders genus *Hogna* are distinguishable based on small somatic and genital differences. Based on habitat preference, these species can broadly be categorized into (i) three "high elevation species" occurring on the volcanic highlands, (ii) three "coastal dry" species occurring in dune habitats along the coast, and (iii) one generalist species which is chiefly found in wet coastal habitats such as salt marshes but also in wet habitats at higher altitudes. To determine the degree of reproductive isolation among these morpho-species, we investigated gene flow among populations and species based on nine allozyme loci. Genetic analysis by means of genetic distance estimates and cluster agglomerative analyses confirmed the status of the defined morpho-species. Allele frequencies were highly similar among populations within a species but differed profoundly among species. Genetic differentiation within the generalist species was generally very low. There were no constant differences between high elevation and coastal populations for this species. Neutral genetic divergence between species appeared to correspond more to geographic distribution rather than to a clear separation of the two different ecological groups within an island. This suggests that a parallel parapatric divergence between high elevation and coastal dry species may have taken place on the oldest islands of San Cristobal and Santa Cruz.

Keywords: Wolf spiders, speciation, island biogeography, ecological speciation

Archipelagos are among the world's great natural laboratories of evolution, as many studies on the Galápagos, Hawaiian, Canary Islands, and other island groups have shown. The Galápagos are of particular interest for the following reasons: they are truly volcanic, well isolated (between 900 and 1000 km west of the Ecuadorian mainland), and of known age (Simkin 1984). There is no evidence of the existence of land bridges so all terrestrial organisms had to cross an oceanic barrier by dispersal from the mainland.

The Galápagos Archipelago consists of 13 large islands and a great number of islets and rocks, all of volcanic origin (Fig. 1). The southeastern islands are the oldest (3–5 million years) while the northern and western islands are the youngest (< 0.7 million years) (Simkin 1984).

Due to geographic isolation, many endemic animal (e.g., Darwin's finches, giant tortoises, lava lizards, mockingbirds) and plant (e.g., *Opuntia* cacti, *Scalesia* trees) groups have radiated. Evolutionary research on these islands has mainly focused on vertebrate species such as Darwin's finches, giant tortoises, lava lizards, mockingbirds, and on plant species such as *Opuntia* cacti and *Scalesia* trees (Grant 1981; Fritts 1984; Snell et al. 1984; Stern & Grant 1996; Rassmann et al. 1997; Cacone et al. 2002). Speciation patterns of invertebrates have been, in contrast, much less studied, and only recently have genetic studies been conducted on Coleoptera such as the tenebrionid *Stomium* (Finston & Peck 1995), the chrysomelid *Nesaecrepidia* (Verdyck & Desender 1999), the carabid *Calosoma* (Desender & Verdyck 2000; Verdyck et al. 2003, 2004), the weevil *Galapaganus* (Sequeira et al. 2000, 2008), and the land snail genus *Bulinulus* (Parent & Crespi, 2006). Genetic studies on Galápagos spiders are presently lacking, while such studies in other locations have revealed adaptive radiations on other archipelagos (e.g., Hawaian *Tetragnatha* spiders, Gillespie 2004; Hawaiian *Dysdera* spiders, Arnedo 2001).

Previous studies on the spider genus *Hogna*, the only wolf spider genus occurring on the archipelago (Maelfait & Baert 1986; Baert & Maelfait 1997), revealed that this genus consists of several closely related, or even cryptic, species. Based on somatic and small genital differences, a total of seven morpho-species is suggested with a distinct distribution on the islands (Baert et al. unpublished data) (Fig. 1). At least three groups of morpho-species can be distinguished that differ distinctly.

A first group of ecologically and morphologically similar morpho-species occur at higher altitudes on the islands in the pampa vegetation zone and are hereafter referred to as "high elevation species." Based on differences in morphology of the genital organs, different species can be distinguished: *Hogna* species 1 (H1), living on both southern volcanoes Cerro Azul and Sierra Negra of Isabela, one of the youngest islands, *Hogna* species 4 (H4) which occurs on islands of intermediate age (Santa Cruz, Santiago, and Volcan Alcedo of Isabela), and *Hogna* species 2 (H2) which occurs on the oldest island of San Cristóbal.

A second group, hereafter referred to as "coastal dry species," lives in the dry arid zone along the coast in vegetated dunes and in the *Opuntia* cactus zone. These morpho-species can only be found on the oldest islands of San Cristóbal (*Hogna* species 5 (H5)), Española (*Hogna* species 7 (H7)), and Santa Cruz (*Hogna species* 6 (H6)). The San Cristóbal species

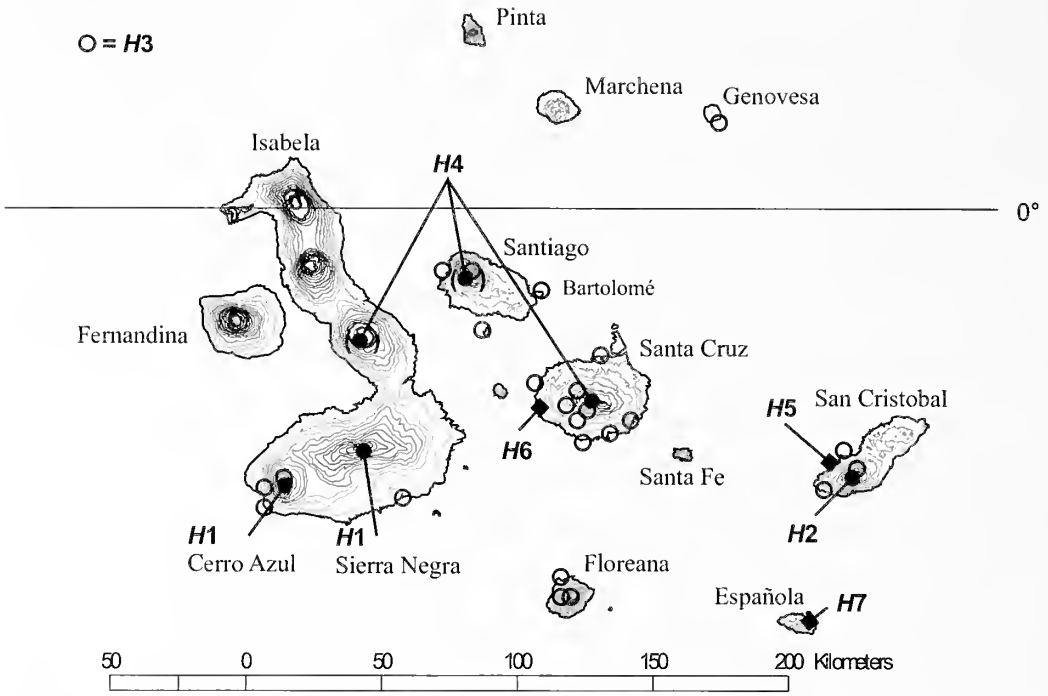

Figure 1.—Map of the sampling locations of the *Hogna* species from Galápagos. Nearby sampling locations are presented as one dot due to space restrictions. Dots between brackets for H4 indicate sites where the species is present but that were not included in this study.

(H5) is mostly found in the depressions overgrown with sea grass (*Sporobolus virginicus*) located behind the shore or on low vegetated dunes, while H7 is found in tall vegetation of the dry arid zone directly adjacent to the littoral zone, but never in the adjacent depressions with salt grass. The Santa Cruz species (H6) is found in the *Opuntia* cactus zone in between dune and pure rocky soil.

The third group comprises populations of the generalist species *Hogna* species 3 that lives in saline habitats along the coast (salt marshes, bays), along permanent pools (e.g., El Chato on Isla Santa Cruz) and in permanent wetlands below 600 m of altitude (e.g., Los Gemelos on Isla Santa Cruz). Scattered populations can also be found above the vegetation inversion zone in wet conditions during El Niño years (characterized by very heavy rainfall giving rise to temporary pools) (Baert & Maelfait 2000). They reach, however, their highest densities in the salt marshes. All these populations have very similar genital organs and are at present interpreted as belonging to a single species. It is widespread over the whole archipelago, with the exception of the northern island Pinta and the southeastern island Española (Baert & Maelfait 1997).

In this paper, we test whether the separation of this genus into seven morpho-species on the Galápagos is justified. By means of cellulose acetate gel electrophoresis, wherein 8 allozyme loci (FUM, G6PDH, GOT, IDH, LDH, MPI, PGI, and PGM) were studied, we investigate whether the genetic variation among species is larger compared to the variation among populations within species and indicative of reproductive isolation among the species.

METHODS

Sampling collection.—In the period between 1996 and 2002, we sampled a total of 43 known Hogna populations (see Table 1) from 9 islands (Santa Cruz, Isabela Volcán Sierra Negra, Isabela Volcán Cerro Azul, San Cristóbal, Floreana, Rábida, Genovesa, Bartolomé, Santiago, and Española) and seven morpho-species. In three localities, the high elevation species occurred sympatrically with H3, [e.g., Cerro Gavillan (populations 40 & 41), El Junco (populations 1 & 2), and Los Gemelos (population 23) (Fig. 1)]. Populations of H4 occurring on the tops of Isabela and Santiago were preserved in ethanol and could therefore not be included in this allozyme study.

Individuals were caught by hand, mostly at sunset with an electric torch worn on the forehead. They were stored and transported in a Taylor-Wharton cryogenic shipper saturated with liquid nitrogen. In the laboratory, the material was stored in an ultra-cold freezer at −80° C. The aim was to investigate at least 40 individuals for each population if possible. In some localities, their densities were so low that this number could not be reached. Some localities were sampled several times but in different years. Voucher specimens are deposited at the Royal Belgian Institute of Natural Sciences.

Allozymes.—Parts of the legs were homogenized in distilled water for performing the cellulose acetate gel electrophoresis, following the procedures of Hebert & Beaton (1989). Eight enzymes (9 loci) were tested for polymorphism: fumarate hydratase (FUM), aspartate minotransferase (GOT1, GOT2), isocitrate dehydrogenase (IDH),lactate dehydrogenase (LDH), mannose phosphate isomerase (MPI), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), and 6-phosphogluconate dehydrogenase (6PGDH).

Allele frequencies were obtained for each population and species. Deviations from Hardy-Weinberg equilibrium were tested by means of an exact test. Genetic divergence between populations and species were estimated based on Nei's unbiased genetic distance (Nei 1978). Based on this distance metric, divergence among populations within species was

Table 1.—List of the 43 sampled *Hogna* populations on Galápagos during the years 1996, 1998, 2000, and 2002. Situation and number of caught specimens per sample. Abbreviations: SCB = Isla San Cristobal; ESP = Española; GEN = Genovesa; SCZ = Santa Cruz; FLO = Floreana; BAR = Bartolomé; RAB = Rabida; SAN = Santiago; ISN = Isabela, Volcan Sierra Negra; ICA = Isabela, Volcán Cerro Azul.

Code	Island	Locality	Vegetation zone	Elevation	Morpho-species	1996	1998	2000	2002
1	SCB	El junco	pampa	675m	*H3*	8			36
2	SCB	El junco	pampa	675m	*H2*	3			44
3	SCB	Cerro San Joaquin	pampa	700m	*H2*				46
4	SCB	Punto Baso	dune	5m	*H5*				41
5	SCB	Punto Baso (fregat nesting)	dune	5m	*H5*				36
6	SCB	Punto Baso (*Sesuvium*)	littoral zone	1m	*H3*				27
7	SCB	Caleta de la Tortuga	littoral zone	5m	*H3*				10
8	SCB	La Lobería	littoral zone	1m	*H3*				42
9	SCB	Caleta Sapho (Spirobolus)	salt grass	1m	*H5*	28			55
10	ESP	Punta Cevallos	dry arid zone	2m	*H7*			40	
11	ESP	Bahía Gardner	dry arid zone	1m	*H7*			31	
12	ESP	Isla Gardner	dry arid zone	2m	*H7*			41	
13	GEN	Lago Arcturus	littoral zone (lagoon)	60m	*H3*			18	
14	SCZ	Laguna Andreas	littoral zone (lagoon)	1m	*H3*	35		42	40
15	SCZ	Bowdich	littoral zone (lagoon)		*H3*				31
16	SCZ	El Garapatero	littoral zone (lagoon)		*H3*			58	22
17	SCZ	Las Palmas	dry arid zone		*H6*				28
18	SCZ	Meteo Station	littoral zone (lagoon)	5m	*H3*		40		
19	SCZ	Bahía Tortuga	littoral zone (lagoon)	1m	*H3*		41	27	53
20	SCZ	Playa Bachas	littoral zone (lagoon)	1m	*H3*		43	40	44
21	SCZ	El Chato	around permanent pool		*H3*			40	40
22	SCZ	El Carmen	temporary pool (El Niño)	350m	*H3*		42		
23	SCZ	Los Gemelos, open	pampa	570m	*H3*				43
24	SCZ	Los Gemelos, Scalesia	*Scalesia* forest		*H3*			47	40
25	SCZ	Media Luna	pampa	600m	*H3*		51	37	27
26	SCZ	Tss ML & Cpunt	pampa		*H4*				13
27	SCZ	Cerro Crocker	pampa	875m	*H4*		42	23	47
28	FLO	Punta Cormoran	littoral zone (lagoon)	1m	*H3*			40	
29	FLO	Finca Cruz	pampa	200m	*H3*			15	
30	FLO	Highland	pampa	350m	*H3*			50	
31	BAR		littoral zone (lagoon)	1m	*H3*		31		
32	RAB		littoral zone (lagoon)	1m	*H3*		38		
33	SAN	Playa Espumila	littoral zone (lagoon)	1m	*H3*		45		40
34	SAN	Aguacate	transition zone (El Niño)	500m	*H3*		40		41
35	SAN	La Central	pampa (El Niño)	700m	*H3*		38		40
36	SAN	Jaboncillo	pampa (El Niño)	820m	*H3*		40		40
37	ISN	Laguna de Villamil	littoral zone (lagoon)	1m	*H3*	41			
38	ISN	Top	pampa		*H1*	42			
39	ICA	Caleta Iguana	littoral zone/dry arid zone	2m	*H3*		32		
40	ICA	Cerro Gavilan	pampa	700m	*H3*		12		
41	ICA	Cerro Gavilan	pampa	700m	*H1*		30		
42	ICA	1100m	dry arid zone (El Niño)	1100m	*H3*		11		
43	ICA	Top	dry arid zone (El Niño)	1530m	*H3*		30		
		Annual total no. specimens				157	606	549	926

compared with the distance among populations of different species. These analyses were performed with the computer packages TFPGA (Miller 1997) and GenAlEx (Peakall and Smouse 2006). Genetic distances were visualized by means of principal component analysis (PCA), designed for ordination of allelic frequency data, by means of the computer package PCA-Gen (Goudet 1999).

RESULTS

Allelic variation and heterozygosity were very low within each speeies, but differed clearly among species, with one or a few alleles that were fixed within the morpho-species. The low genetic variability among populations within species, compared to the variability among species, is clearly depicted when genetic distances are compared among populations (Table 2). The genetic distance between populations belonging to the same morpho-species ranged from 0 to maximum 0.031 (H3), demonstrating that the allele frequencies of the different populations within a given morpho-species were highly similar. Differences in allele frequency of populations belonging to a different morpho-species were, in contrast, considerably higher and ranged from 0.118 to 2.277. The smallest genetic distances were observed between H2 ("high elevation" San Cristobal) and H7 ("coastal dry" Española) and between H5 ("coastal dry" San Cristobal) and H7.

Allele frequencies for all loci were near to fixation for almost all morph-species (Table 3). None of the species

Table 2.—Genetic distance data for seven *Hogna* morpho-species on the Galápagos. Above diagonal: genetic distances between the different morpho-species when allele frequencies of the different populations of each morpho-species were pooled; diagonal: minimum and maximum genetic distance between populations of the same morpho-species; below diagonal: minimum and maximum genetic distance between populations of different morpho-species.

	H1	H2	H3	H4	H5	H6	H7
H1	**0.012**	1.711	1.026	0.449	1.218	1.089	1.719
H2	1.647–1.811	**0.0016**	2.059	0.587	0.267	1.151	0.131
H3	0.910–1.040	1.614–2.154	**0.000–0.031**	1.481	1.474	1.090	2.193
H4	0.435–0.483	0.577–0.600	1.230–1.504	**0.0001**	0.577	0.603	0.800
H5	1.179–1.281	0.260–0.275	1.213–1.503	0.575–0.584	**0–0.0001**	0.817	0.125
H6	1.084–1.097	1.123–1.182	1.083–1.235	0.602–0.607	0.813–0.822	—	1.119
H7	1.645–1.841	0.122–0.146	1.727–2.277	0.798–0.811	0.118–0.138	1.121–0.122	**0.000–0.013**

comparisons resulted in fixation of the same alleles, and each morpho-species was, therefore, characterized by a unique allele combination.

The low differences among conspecific populations compared to differences among morpho-species were also obtained from PCA ordination of the different populations (Fig. 2). The first three axes explained 74.24%, 15.06%, and 4.06% of the total allelic variation respectively. Along the first axis, the H3 populations are clearly separated from the other morpho-species. The position of the remaining species along

Table 3.—Allele frequency data for seven *Hogna* morpho-species on the Galápagos.

		H1	H2	H3	H4	H5	H6	H7
Npop		2	2	30	2	3	1	3
Nind		72	91	1632	144	112	28	153
FUM	1	0.0000	0.0000	0.0000	0.0035	0.0000	1.000	0.0000
	2	0.9931	0.0000	0.0000	0.9896	0.0000	0.0000	0.0000
	3	0.0000	0.9890	0.0000	0.0035	1.0000	0.0000	1.0000
	4	0.0069	0.0110	1.0000	0.0035	0.0000	0.0000	0.0000
GOT1	1	0.0000	0.0165	0.0000	0.0000	0.0000	0.0000	0.0033
	2	0.0278	0.9560	0.0018	1.0000	1.0000	1.0000	0.9967
	3	0.9722	0.0220	0.9982	0.0000	0.0000	0.0000	0.0000
	4	0.0000	0.0055	0.0000	0.0000	0.0000	0.0000	0.0000
LDH	1	1.0000	0.0000	0.9997	0.0035	0.0000	0.0000	0.0000
	2	0.0000	0.0000	0.0000	0.0069	1.0000	0.0000	1.0000
	3	0.0000	1.0000	0.0003	0.9861	0.0000	0.0000	0.0000
	4	0.0000	0.0000	0.0000	0.0035	0.0000	1.0000	0.0000
G6P3H	1	0.0000	1.0000	0.0003	0.0000	0.0000	0.0000	1.0000
	2	1.0000	0.0000	0.9994	0.9931	1.0000	1.0000	0.0000
	3	0.0000	0.0000	0.0003	0.0069	0.0000	0.0000	0.0000
MPI	1	0.0000	0.0714	0.9997	0.0035	0.0045	0.0000	0.0000
	2	0.0000	0.9286	0.0003	0.0070	0.9955	0.0000	1.0000
	3	1.0000	0.0000	0.0000	0.9860	0.0000	0.0000	0.0000
	4	0.0000	0.0000	0.0000	0.0035	0.0000	1.0000	0.0000
PGI	1	0.0000	0.0330	0.0003	0.0139	0.0000	0.0179	0.0000
	2	0.0069	0.8791	0.9988	0.9549	0.9911	0.9286	0.9412
	3	0.0139	0.0824	0.0009	0.0174	0.0089	0.0536	0.0588
	4	0.9583	0.0000	0.0000	0.0139	0.0000	0.0000	0.0000
	5	0.0208	0.0055	0.0000	0.0000	0.0000	0.0000	0.0000
PGM	1	0.0000	0.0275	0.9969	0.0035	0.0000	0.0536	0.0000
	2	0.0278	0.9341	0.0031	0.0000	0.9688	0.0000	0.8170
	3	0.9722	0.0330	0.0000	0.9931	0.0313	0.9464	0.0065
	4	0.0000	0.0055	0.0000	0.0035	0.0000	0.0000	0.1765
GOT2	1	0.0625	0.0495	0.9991	0.0069	0.0089	0.0000	0.0000
	2	0.9375	0.9286	0.0009	0.9861	0.9911	0.9286	1.0000
	3	0.0000	0.0220	0.0000	0.0069	0.0000	0.0714	0.0000
IDH1	1	0.0000	0.0000	0.9694	0.0104	0.0000	1.0000	0.0000
	2	0.5000	1.0000	0.0306	0.9896	1.0000	0.0000	1.0000
	3	0.5000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

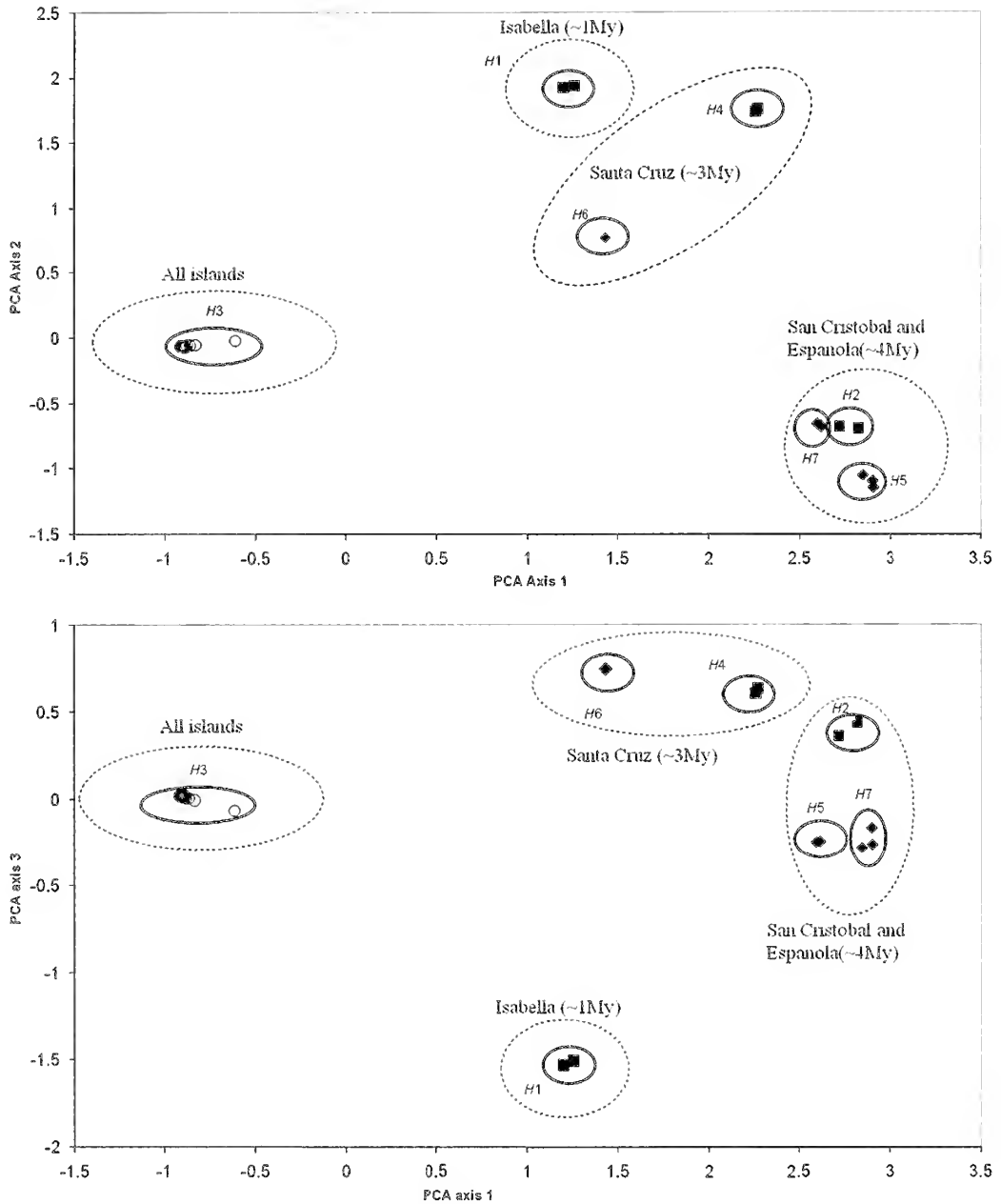

Figure 2.—Results of principal component analysis (axes 1, 2 and 3). (Filled squares = high elevation species; filled diamonds = coastal dry species; open circles = generalist species.)

this axis and the second axis corresponded to their geographic position and age of the islands rather than to their habitat preference. The three species of the oldest islands – H7 from Española and H2 and H5 from San Cristobal – were clustered in the PCA, followed by H4 and H6 from Santa Cruz and H1 from the volcanoes Cerro Azul and Sierra Negra on Isabela.

DISCUSSION

Our results show that there is a clear and very high degree of genetic divergence between the previously defined morpho-species. Moreover, genetic divergence among populations within species was much lower (Table 2, Fig. 2). These two findings indicate that these morpho-species likely represent distinct reproductively isolated species.

Although the validity of allozymes for phylogenetic inferences is questionable since the historical and genealogical relationship between the different alleles remains unknown (Lowe et al. 2004), a few suggestions concerning historical patterns of divergence can be deduced.

First, these results suggest that *Hogna* speciation on the Galápagos is likely due the combined effect of geographic isolation and ecological specialization within the different climatological and vegetation zones present on the different islands. Except for H3, species from the same or proximate island tend to be genetically more similar to each other. Species living on the same islands but in different habitats are, however, genetically fixed for a few loci, clearly indicating a lack of gene flow and hence strong reproductive isolation. Combining these results suggests that ecological specialization

on the islands Santa Cruz and San Cristobal occurred repeatedly in association with speciation events rather than a diversification of a habitat adapted lineage with secondary colonization of the specialized forms to the different islands. According to the second scenario, species living in the same habitat would then be expected to be genetically more similar to each other.

Similar patterns of species diversification in terms of geographic position and ecological specialization have been confirmed by more thorough genetic analyses of *Tetragnatha* spiders from Hawai (Gillespie 2004). In the Galápagos, this speciation pattern has been observed in other terrestrial invertebrates such as weevils and snails (Parent & Crespi 2006; Sequiera et al. 2008).

Whether the generalist species H3 can be regarded as closely related to the ancestral species, as suggested by Baert & Maelfait (2000), however, cannot be confirmed by these data. The smaller genetic distance between the generalist H3 and the species from younger islands (H1) compared to those of older islands (H2, H5, and H7) is in accordance with this hypothesis. Surprisingly however, H3 showed a very low degree of genetic variation within populations. Moreover, distant populations as well as populations living in different habitats all appeared to be genetically very homogenous. These observations suggest that this generalist and apparently highly dispersive species may have colonized the archipelago independently.

The results can only be interpreted as preliminary as they are based on allozyme data and only a few loci were scored. Moreover, the selective neutrality of allozymes has often been questioned. Our ongoing work aims to add more variable loci such as mitochondrial DNA (Cytochrome Oxidase I) so that more well founded phylogenetic inferences can be made. Also, future work should include *Hogna* species from the South American mainland to better understand the phylogenetic relationships between the species and the colonization history of *Hogna* in Galápagos.

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Tenacity and silk investment of two orb weavers: considerations about diversification of the Araneoidea

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Abstract. Orbiculariae consists of two major clades: the cribellate Deinopoidea and the much more diverse ecribellate Araneoidea. It has been hypothesized that the higher diversity of Araneoidea is a consequence of the superiority of the viscid orb web. However, this explanation seems incomplete; for example, cribellate silk may perform better than viscid silk in some contexts. Here, we consider the hypothesis that the diversification of Araneoidea was facilitated by changes in microhabitat occupation behavior due to the eheaper viscid orb web. In the present work we investigate the idea that the reduction in site tenacity caused by the emergence of the viscid orb web has led to an increase in the exploration of different resources and to a greater diversification of the Araneoidea through the evolutionary time. To test this idea, we evaluated the response of one cribellate orb web spider (*Zosis geniculata* Olivier 1789, Uloboridae) and one ecribellate orb web spider (*Metazygia rogenhoferi* Keyserling 1878, Araneidae) to abrupt prey absence. The changes in site tenacity and the day-to-day investment in web silk were evaluated. Spiders with three-dimensional webs tend to exhibit greater site tenacity than spiders making orb webs. *Zosis geniculata* and *M. rogenhoferi* show similar site tenacity when prey is ample. When prey is unavailable, the tenacity of the cribellate species increases while the tenacity of the ecribellate remains unchanged, and the silk investment of both species decreases. However, this decrease in silk investment is more extensive in *Z. geniculata*. These results coincide with the idea that a less costly ecribellate orb web leads to a lower tenacity and suggest that more frequent microhabitat abandonment in a context of insect radiation (Neoptera) leads to more diverse and opportunistic exploration of mierohabitats that, in the long term, may be one explanation for the greater Araneoidea diversification.

Keywords: cribellate, evolution, Araneidae, Uloboridae, spiders

Resumo. Orbiculariae é composto por dois grandes clados de aranhas, as cribeladas Deinopoidea e as não cribeladas e muito mais deiversas Araneoidea. A hipótese mais aceita é a de que a maior diversificação do grupo ecribelado (Araneoidea) é devido à superioridade da teia orbicular viscosa. Porém, essa explicação não é suficiente para explicar a diversificação de Araneoidea já que o fio cribelado, por exemplo, pode ser mais eficiente em alguns contextos ecológicos. Assim, consideramos a hipótese de que a diversificação de Araneoidea foi facilitado pela redução na tenacidade pelo microlocal, conseqüência do surgimento de uma teia de fio viscoso mais barato. Para começar a explorar essa idéia nós avaliamos a resposta de uma espécie cribelada (*Zosis geniculata* Olivier 1789, Uloboridae) e de uma ecribelada (*Metazygia rogenhoferi* Keyserling 1878, Araneidae) a um evento de indisponibilidade de presas. Acompanhamos as mudanças na tenacidade e no investimento em seda dia-a-dia. As aranhas construtoras de teias caras tendem a apresentar maior tenacidade pelo microlocal do que as construtoras de teias baratas. Orbitelas cribeladas e ecribeladas também apresentam diferentes investimentos na construção e manutenção da teia. Com a ingestão regular de presas *Z. geniculata* e *M. rogenhoferi* apresentam tenacidades similares. Quando cessa a oferta de presas, a tenacidade da espéeie cribelada aumenta enquanto a espécie ecribelada mantém-se inalterada, porém, o investimento em seda de ambas diminui, e *Z. geniculata* reduz mais intensamente o investimento em seda. A maior freqüência no abandono da teia teria permitido, de modo oportunístico, uma maior e mais rápida exploração de recursos novos advindos da radiação do grupo de insetos alados modernos. O efeito dessa maior mobilidade pelo ambiente, ao longo do tempo evolutivo, poderia ajudar a explicar a radiação de Araneoidea em relação a seu grupo-irmão cribelado.

Palavras-chave: cribeladas, evolução, Araneidae, Uloboridae, aranhas

Current hypotheses about the extreme diversification of araneoid orb weavers investigate synapomorphies of the group as putative key adaptations. Web features such as orb verticality (Eberhard 1989; Opell et al. 2006) or the presence of viscid silk (Bond & Opell 1998) have been suggested as possible innovations causally related to species diversification. Better adhesiveness and extensibility (Köhler & Vollrath 1995), lower cost (Opell 1996, 1998), or low UV reflectance (Craig et al. 1994) have all been investigated as features that potentially have enhanced the fitness of viscid orb weavers as opposed to the primitively cribellate deinopoids. Nevertheless, these hypotheses are vague in suggesting how this specific improvement in performance affects fitness since they did not discuss the context by which they are proposed to increase fitness. Some cribellate orb weavers, for example, also spin vertical webs (Lubin 1986); viscid threads are not necessarily more adhesive (Opell 1996, 1998) or extensible (Opell & Bond 2000; Blackledge & Hayashi 2006) than cribellate silk; high UV reflectance can also enhance fitness by attracting insects (Craig & Ebert 1994; Watanabe 1999; Li et al. 2004) or being a defense against predators (Craig & Freeman 1991; Zschokke 2002; Bruce et al. 2005). In this paper, we offer a previously unexplored hypothesis: changes in site tenacity could have contributed to Araneoidea radiation.

Vollrath & Selden (2007) suggest that orb web spider evolution might be a predator-prey arms race concurrent with the rise of the modern flying insects (pterygote Neoptera). In this evolutionary scenario, cribellate and viscid orbweavers

began with different potentials to take advantage of the new resources where a less costly and more quickly built web, along with the lower tenacity, might have given viscid orbweavers a competitive edge. Even in current orb web spiders, we can find indications of this ancient behavioral flexibility. Some orb weavers are not restricted to web site choice rules (Eberhard 1971). Thus we should expect a reduction in site tenacity to be associated with a more widespread occupation of the habitat. Reduced site tenacity should result in the occupation of a larger range of microhabitats, leading to more opportunities for speciation. We propose that the more diverse clade of ecribellate orb weavers will have lower site tenacity in relation to the less diverse clade of cribellate orb weavers.

Site tenacity varies in response to ecological conditions. Desert spiders present higher tenacity, either from being subjected to a high physiological stress, or because of a relatively high risk of not reaching a new suitable site (Riechert & Gillespie 1986; Henschel & Lubin 1997). Web damage raises the chances of site abandonment (Gillespie & Caraco 1987), and abandonment occurs earlier from webs with a high production cost (Eberhard 1971) than on low cost webs (Craig 1989). In general, high cost of the sheet webs compared to the orb webs is also associated with a higher tenacity (Janetos 1986; Riechert & Gillespie 1986).

The association of changes in web costs with changes in site tenacity shows that ecological factors are not solely responsible for site abandonment. General evolutionary changes in web building and architecture (web costs) could be associated with general phylogenetic patterns of site tenacity. Several indirect evidences point to an evolutionary change from a high cost orb web among cribellate deinopoids (Uloboridae plus Deinopidae) to a low cost orb web in the remaining Orbiculariae clade. The duration of a web building bout ranges from 3 to 5 h among the cribellate orb weavers to about 30 min among the ecribellate araneids (Lubin 1986; Zschokke & Vollrath 1995a,b). The energy consumption must be higher among uloborids since the building of the cribellate adhesive spiral requires intense and repetitive combing movements of legs IV (Eberhard 1988), an unnecessary behavior among ecribellate orb weavers (Peakall & Witt 1976). The cribellate silk is highly proteic, much more so than the 80% water volume viscous droplets from the ecribellate orb weavers (Crews & Opell 2006). Finally, cribellate spiders recycle less of their silk than ecribellate ones (Lubin 1986; Opell 1998).

Here, we evaluate the hypothesis that the diversification of ecribellate orb weavers may in part result from an evolutionary reduction in site tenacity that could have led to a faster and more opportunistic exploitation of unpredictable resources, thus facilitating the diversification in the clade. As a first step in the evaluation of this new hypothesis, in this paper we test the idea that lowered costs in orb web building and maintenance are associated with lowered tenacity values. In order to explore this new hypothesis, we performed a preliminary survey to compare a cribellate and an ecribellate orb weaver species in relation to their site tenaeity and silk investment.

METHODS

We chose *Zosis geniculata* Olivier 1789 (Uloboridae) and *Metazygia rogenhoferi* Keyserling 1878 (Araneidae) as representatives of the cribellate and ecribellate orb weavers, respectively. The choice was based on several common factors of these species. Both species have similar adult body sizes, they spin similar size orb webs, they do not present marked seasonality, and their families are at the base of the sister clades Deinopoidea (cribellate) and Araneoidea (ecribellate). The specimens were collected in São Paulo city, and voucher specimens were deposited in the arachnological collection at Instituto Butantan (IB-88434 to IB-88452; *M. rogenhoferi* plus nematodes IB-88441, IB-88439, IB-88622; A.D. Brescovit, curator).

Adaptation to laboratory conditions.—We brought adult females to the laboratory and kept them in individual acrylic boxes (31 × 31 × 12 cm) in a room with inverted day-night cycle (12 h dark:12 h light) and low temperature (24° to 26° C) and humidity (76% to 81% RH) variation. After building their first webs, the spiders were marked with gouache ink and overfed with a diet of crickets (of the same size of the spiders, mean weight = 7.23 ± 0.50 mg, $n = 10$) three times a week for at least 20 days, until the spiders built webs regularly in the boxes. Many *Metazygia rogenhoferi* specimens died in the first week of feeding, due to nematode or fungal parasitism. After the first week in the laboratory, no more spiders died due to parasitism.

Experimental procedure.—After the spiders adapted to laboratory conditions, we separated 40 spiders (20 of each species) for the experiment. They each were fed one cricket before their acrylic boxes were opened so that they could now leave the original web building site. In this free condition, spiders were fed one cricket (of the same size as the spider) every four days. The food was repeated five times in succession (totaling 21 "Fed" days = F condition); subsequently feeding was abruptly interrupted for the rest of the experiment (the "Unfed" = U condition), which continued until all spiders had left the original web site. This change in diet was planned in order to induce site abandonment in the laboratory so that we could compare abandon times between the species under controlled conditions. Thus we measured the tenacity by the number of days from the opening of the acrylic box until the abandonment of the web for each spider. Also, we measured, for both treatments (F and U) and each spider species, the cumulative investment obtained through the sum of the length of all capture spiral reconstructions over each 21-day treatment period. Every day we also measured, for each reconstruction, the length of the adhesive spiral on the reconstruction (cm), the area reconstructed (cm^2), the total area of the final web (old plus reconstructed portions), and the adhesive thread density in the reconstruction (cm/cm^2). We used the mean of the successive webs from each individual spider in each 21-day treatment period to proceed with the analysis. We assumed that thread thickness and amount of glue were constant. This provided only an approximate estimate of investment since the amount of glue may often change (Crews & Opell 2006). Web measures were taken from digitized photographs with the aid of the freeware UTHSCSA Image Tool 3.0 (http://ddsdx.uthscsa.edu/dig/itdesc.html). Each reconstruction was identified by comparing radius and spirals at the hub with those immediately before web reconstruction pictures (Fig. 1).

Statistical analysis.—We used the Kaplan-Meier procedure (Motulsky 1995) to estimate, for each species, the probability

of remaining at the original web site (the acrylic box), as a function of the time since the beginning of the experiment (i.e., the tenacity function). In this analysis, individuals who died before leaving the original web site are considered censored data. A prerequisite of the Kaplan-Meier procedure is that the number of censored individuals is not correlated with the survival function itself, that is, that the death of the subjects is not correlated with the treatment. Although this prerequisite was certainly valid at the beginning of the unfed treatment, this was not so after a long period of starvation. In order to overcome this difficulty, we excluded from the comparison all tenacity measurements after a strong reduction in the size of the abdomen of the spiders (after 28 days of starvation). We expected the uloborid to have a higher probability of staying in the original web site, meaning a higher tenacity. The Breslow statistic (Motulsky 1995) was used to test for differences in tenacity between the two species. The Breslow test is more conservative than other similar tests (Log-Rank and Tarone-Ware), and also more appropriate, since the tenacity functions in our experiment do not vary proportionately to each other (Gross & Clark 1975).The differences in silk investment between treatments (F and U) were tested, for each species, with the t-test or Wilcoxon statistic. Differences in silk investment between speeies, either in the F or in the U condition, were tested through the paired t-test or Mann-Whitney statistic (Fowler et al. 1998). Only spiders that did not abandon the acrylic boxes during the 21-day U treatment period were considered in the investment analyses. In order to render silk investment under the two conditions (F and U) comparable, we used only the data from the first 21 days in the Unfed condition (to equal the 21 days in the F condition). Statistical analyses were performed with the software packages SPSS 13.0 (Kaplan Meier and Breslow) and Statistica 7.0 (for silk investment). We considered $\alpha = 0.05$ as the critical level of significance for all statistical tests.

RESULTS

Web site tenacity.—While the araneid and the uloborid do not differ in the probability of leaving the web site under the fed condition (Breslow = 0.069; $P = 0.792$; $n = 40$) when unfed, the uloborid is more tenacious than the araneid (Breslow = 4.956; $P = 0.026$; $n = 27$). *Metazygia rogenhoferi* does not seem to alter its tenacity in response to hunger and the probability of leaving the web site declined almost steadily throughout the experimental period. *Zosis geniculata*, however, presented periods of maintenance and periods of abrupt decline in the probability of leaving the web site (Fig. 2). *Zosis geniculata* remained for longer starvation periods; the last *Z. geniculata* left the web site after 75 days without food, while the last *M. rogenhoferi* abandoned her web site after 57 days without food.

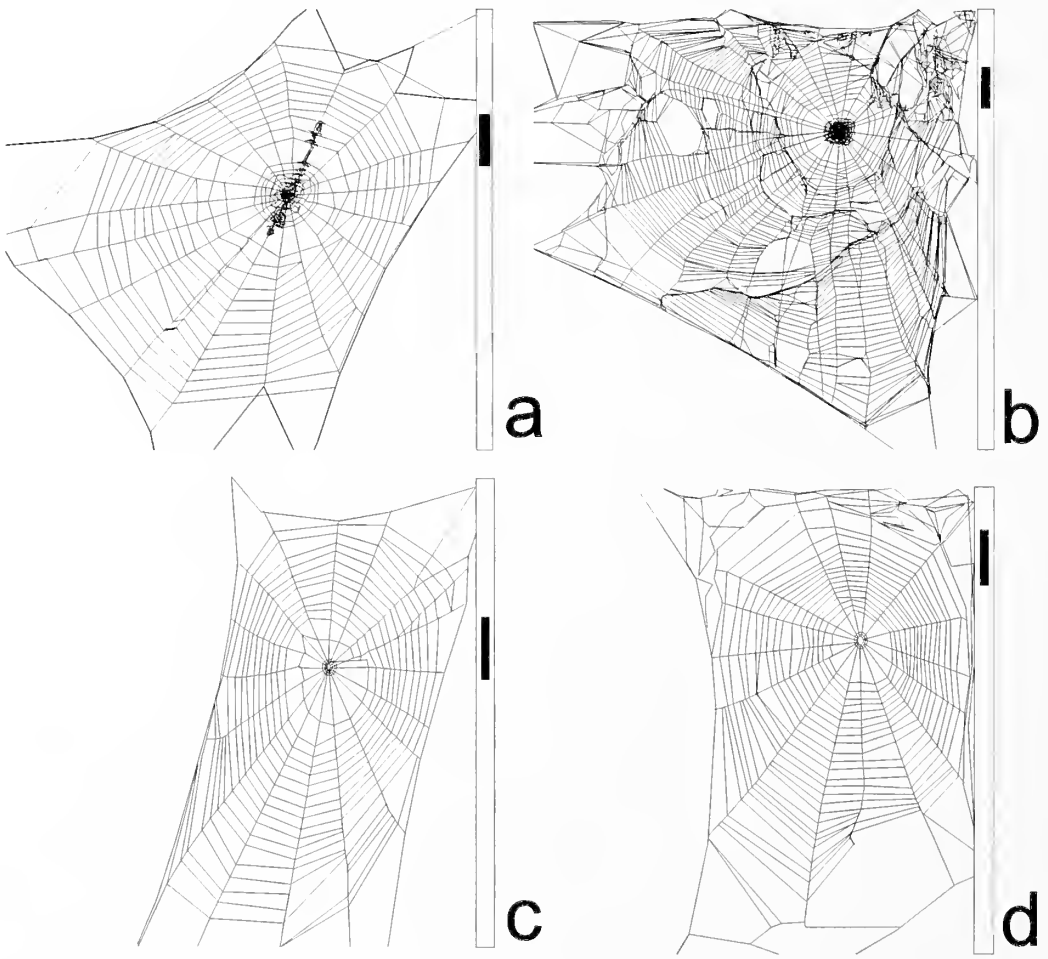

Figure 1.—Drawings based on photographs of webs, illustrating the first web of *Z. geniculata* (a) and *M. rogenhoferi* (c) and partial reconstructions (b and d, respectively).

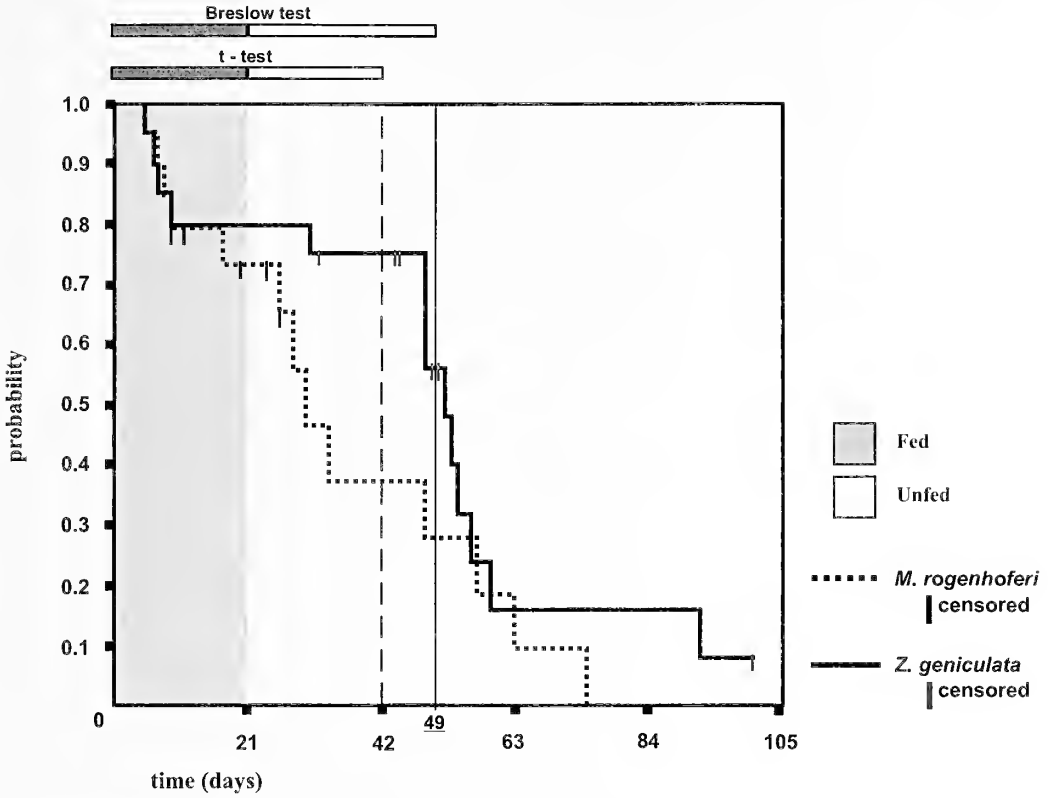

Figure 2.—Permanence probability curves obtained with the Kaplan-Meier Procedure from survival analysis statistics. Upper bars shows the periods used in the comparative statistical analysis.

Table 1.—Web measurements and reconstruction frequencies from *M. rogenhoferi* and *Z. geniculata* (mean and standard deviation) of individuals after 21 days on the Fed and the Unfed periods.

		Fed		Unfed	
Species	Measurements	Mean	SD	Mean	SD
Metazygia rogenhoferi	**reconstruction frequency**	8	2.99	6	1.26
	cumulative capture spiral length (cm)	5206.93	2584.64	3774.47	1535.07
	capture spiral length (cm/web)	718.92	143.81	655.47	112.24
	reconstructed area (cm^2)	272.64	66.77	315.51	79.34
	total web area (cm^2)	388.50	106.39	414.89	80.43
	threads density (cm/cm^2)	2.33	0.38	2.11	0.17
Zosis geniculata	**reconstruction frequency**	6	1.91	2	1.10
	cumulative capture spiral length (cm)	2278.17	1311.88	424.26	317.29
	capture spiral length (cm/web)	333.08	130.17	188.05	134.73
	reconstructed area (cm^2)	120.54	42.31	73.16	49.30
	total web area (cm^2)	304.30	112.13	445.54	137.89
	threads density (cm/cm^2)	2.77	0.61	2.89	0.82

Silk investment.—All the measurement results are summarized in Table 1 and correspond only to spiders that did not abandon the acrylic boxes in the 21-day U treatment period. The different feeding regimes do not alter the measured parameters of the web of *M. rogenhoferi* ($n = 4$ for all tests). Neither the linear cumulative silk investment ($t = 2.017$; $P = 0.137$) as in mean thread investment per web ($t = -0.100$; $P = 0.926$), nor the web reconstruction area ($t = -2.906$; $P = 0.062$), total web area ($t = -0.567$; $P = 0.610$), adhesive thread density ($t = 2.390$; $P = 0.097$), or the frequency of web reconstruction ($Z = 1.604$; $P = 0.109$) change with diet. In contrast, *Z. geniculata* ($n = 14$ for all tests) reduced silk investment, diminishing the linear adhesive thread cumulative investment ($t = 5.806$; $P < 0{,}001$) as in mean thread investment per web ($t = 2.808$; $P = 0.015$), web reconstruction area ($t = 2.794$; $P = 0.015$), total area ($t = -6.580$; $P < 0.001$), and the frequency of web reconstruction ($Z = 3.296$; $P = 0.001$) without altering adhesive thread density ($t = -0.575$; $P = 0.575$).

Species differ in most web parameters ($n = 18$ for all tests). Fed *M. rogenhoferi* reconstructed larger portions of their webs (reconstruction area: $t = 5.157$; $P < 0.001$) and invested more adhesive silk in terms of mean spiral length per web ($t = 3.947$; $P = 0.001$) than did *Z. geniculata*, although the total web area

(t = 1.122; P = 0.278), cumulative linear investment (t = 2.295; df = 3,5; P = 0.094*), adhesive thread density (t = −1.077; P = 0.298) and the frequency of reconstructions (Z = 1,076; P = 0.327) is similar between species. Unfed *M. rogenhoferi* also reconstructed larger portions of their webs than did *Z. geniculata* (reconstruction area: t = 7.700; P < 0.001) although the total web area is again similar between species (t = −0.457; P = 0.653). *Metazygia rogenhoferi* invested more adhesive silk in terms of cumulative linear investment (t = 4.880; df = 3,1; P = 0.016*) and mean spiral length per web (t = 6.077; P < 0.001) than did *Z. geniculata*. *Metazygia rogenhoferi* produced a slightly denser mesh of adhesive threads (t = −2.165; P = 0.046) than that of *Z. geniculata*, but the P-value could be less or even not significant if we had a greater sample.

DISCUSSION

Web site tenacity.—The cribellate *Z. geniculata* is more tenacious than the ecribellate *M. rogenhoferi*, the former seeming quite indifferent to changes in diet. On the one hand, *Zosis geniculata* began to abandon their webs only after a long period of starvation, a pattern also observed among other costly web weavers, such as the ecribellate, giant nephilid orbweavers (Vollrath 1985; Vollrath & Houston 1986) or some sheetweb weavers (Janetos 1982, 1986). On the other hand, the deinopoid clade also presented some web reductions associated with more mobile species (Lubin 1986). High tenacity seems thus to be associated with costly webs, independent of the type of adhesive thread, viscid or otherwise. These results give support to the hypothesis that the high diversity of Araneoidea is not simply the result of the discovery and use of viscid threads. The evolutionary reduction of site tenacity, made possible after the appearance of a less costly orb web (see below), could be a mechanism facilitating speciation, because it allowed a fast and opportunistic exploitation of new resources that is the ancestral condition promoting orb web spider high Triassic diversification (Vollrath & Selden 2007).

Silk investment.—In general, *M. rogenhoferi* is less responsive to a reduction in diet than *Z. geniculata*. While the uloborid species decreases silk investment, the araneid species does not alter its web investment, at least not in terms of the total length of silk (we did not test if thickness of threads or amount of glue changed). The results with *M. rogenhoferi* contradict previous studies with ecribellate orb weavers. Sherman (1994) showed that hungrier *Larinioides cornutus* (Clerck 1757) (Araneidae) invest more effort in foraging (web), and Higgins & Buskirk (1992) showed that *Nephila clavipes* (L. 1757) (Nephilidae) build larger orbs during times of decreased prey capture. Nevertheless, Crews & Opell (2006) found that *Cyclosa turbinata* (Walckenaer 1842) (Araneidae) does not change the investment in capture silk length, but progressively decreases its adhesive silk investment (less hygroscopic compounds) in successive webs built in harsh unfed conditions. Thus the literature does not present a simple pattern, probably as a result of the use of different feeding regimes in the different studies. It is not unreasonable for these orb weavers to present contradicting responses to different levels of starvation since it is not unusual to find nonlinear reaction norms (Schlichting & Pigliucci 1998). Therefore, these contradictory data can be the result of different researchers inspecting different regions of the same nonlinear reaction norm.

The goal of the present paper, however, was not to compare cribellate versus ecribellate complete reaction norms, but rather to test predictions in a more narrow phenotypic space. In this narrower context, we expected that the more costly webs of the uloborid would lead to a more conservative strategy, and the reduction in silk investment is in accord with this prediction. *Zosis geniculata* is able to reduce silk investment in response to reductions in prey number because of the properties of its adhesive thread. Cribellate silk keeps its adhesiveness longer than ecribellate silk (Eberhard 1980; Peters 1987; Sherman 1994, but see Opell & Schwend 2008), so that the web remains functional for longer periods, and the spider does not need to fully destroy the previous web in order to reconstruct the next one. At each reconstruction, the spider destroys only a part of the old web where it builds the new one; the final trap is a composition of many successive reconstructions. Eberhard (1971) observed a similar reconstruction pattern in *Uloborus diversus* Marx 1898 (Uloboridae), so it seems that these cribellate orb weavers handle reductions in prey supply using their longer lasting capture thread. They can reduce costs by staying at the same site and keeping the old trap for a longer period, a strategy that may not work well with the short lasting webs of the ecribellate orb weavers. In this way, silk investment is tied to web site tenacity. These cheap viscid orb weavers and wandering spiders may have had an advantage in relation to their cribellate counterparts during the spread of new prey resources during the Neopteran radiation (Vollrath & Selden 2007).

Other considerations.—Bond & Opell (1998) showed that the Araneoidea clade is statistically more diversified in species number than its sister group, the Deinopoidea, arguing that it was due to a key innovation: the invention of the viscid thread. According to Vollrath & Selden (2007) a flexible behavior lead to a faster exploration of new resources and the fine performance adaptations came after. So, we have suggested that our web site tenacity hypothesis is one possible flexible behavioral component that drives the orb web spider evolution followed by "morphological" (web) fine performance adaptation.

A recent phylogeny of Nephilidae (57 species, Kuntner et al. 2008) proposes that these spiders could be sister to the remaining Araneoidea (11199 species, Platnick 2008). Using the analysis proposed by Slowinski & Guyer (1993), we can see a clade imbalance, with the "remaining Araneoidea" being much more speciose than the family Nephilidae (P = 0.005). Thus, if this new positioning of Nephilidae proves to be correct, the greater species richness of Araneoidea would be associated with a clade within Araneoidea where the viscid thread is plesiomorphic.

Besides using a viscid thread, nephilids build unusually large webs. That a nephilid reconstructs only a sector of its web each time indicates that this web is costly and that it is economizing (Nentwig & Spiegel 1986). Also, most nephilids build other costly silken structures that are presumably not recycled (Kuntner 2006; Kuntner et al. 2008). Probably as a result of this costly web, these spiders also present high web site tenacity, even when subjected to a few prey (Vollrath 1985; Vollrath & Houston 1986).

Our comparison of two species, even ones carefully chosen to have similar life cycle, size, and web characteristics, certainly is not sufficient to establish broad trends. However,

our findings offer small but important experimental support for a novel hypothesis. Considering all the facts presented, we suggest that one of the factors driving the diversification of the Araneoidea clade might be the site tenacity reduction allowed by the less costly araneids' viscid webs, a complementary hypothesis to the widespread evolutionary explanations that present only the viscid silk performance as the main key innovation of orb weavers.

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Revision of the theraphosid spiders from China (Araneae: Mygalomorphae)

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Abstract. Ten theraphosid spiders of the genera *Citharognathus* Pocock 1895, *Haplopelma* Simon 1892, *Chilobrachys* Karsch 1891, *Yamia* Kishida 1920 and *Selenocosmia* Ausserer 1871 from China are described, including four new species, namely *Selenocosmia xinping* sp. nov., *S. jiafu* sp. nov., *S. xinhuaensis* sp. nov., and *Chilobrachys liboensis* sp. nov. *Plesiophrictus guangxiensis* is transferred to the genus *Chilobrachys*. Additionally, the species *Chilobrachys jingzhao* Zhu, Song & Li, 2001 is newly synonymized with *Chilobrachys guangxiensis* (Yin & Tan 2000).

Keywords: New species, new combination, new synonymy, taxonomy

Spiders of the family Theraphosidae are medium to large species, some of which live in holes in trees protected by a thick sheet web, but most inhabit a ground burrow. The hole may be lightly silked over, but is never covered with a door (Murphy & Murphy 2000). All the theraphosid spiders are listed as "protected" animals in China (Wang & Xie 2005). Theraphosidae is a large family comprising 113 genera and 900 species worldwide (Platnick 2008), with tropical and subtropical distributions. Currently, Theraphosidae in China includes two subfamilies, five genera and ten species, including one newly recorded genus and four new species reported herein. The genera and species revised are: *Citharognathus* Pocock 1895, with one species: *C. tongmianensis* Zhu, Li & Song 2002; Haplopelma Simon 1892, with two species: *H. hainanum* (Liang et al. 1999) and *H. schmidti* von Wirth 1991; *Chilobrachys* Karsch 1891, with three species: *C. hubei* Song & Zhao 1988, *C. guangxiensis* (Yin & Tan 2000) newly transferred here from the genus *Plesiophrictus*, and *C. liboensis* sp. nov. from Guizhou Province, China; *Yamia* Kishida 1920, with one species: *Y. watasei* Kishida 1920; and *Selenocosmia* Ausserer 1871, which is recorded from China for the first time, with three new species: *S. xinping* sp. nov. from Hongkong, *S. jiafu* sp. nov. and *S. xinhuaensis* sp. nov. both from Yunnan. Also, the species *Chilobrachys jingzhao* Zhu, Song & Li 2001 is considered a junior synonymy of *Chilobrachys guangxiensis* (Yin & Tan 2000).

METHODS

Ilustrations and measurements were produced using a Tech XTL-II stereomicroscope equipped with an Abbe drawing device and an ocular micrometer. All measurements are given in millimeters. Carapace length was measured from the anterior margin to the rear margin of the carapace medially. Female genitalia were cleared in a warm 10% solution of potassium hydroxide (KOH), transferred to alcohol and temporarily mounted for drawing.

The following abbreviations are used: ALE, anterior lateral eyes; AME, anterior median eyes; MOA, median ocular area; PLE, posterior lateral eyes; PME, posterior median eyes. PMS, posterior median spinneret; PLS, posterior lateral spinneret. Depositories include Institute of Zoology, Academia Sinica, Beijing, China (IZB); Faculty of Life Sciences, Hunan Normal University, Changsha, China (HNU); Museum of Hebei University, Baoding, China (MHBU); Senckenberg Museum Frankfurt (SMF); and Zoologische Staatssammlung München (ZSM).

TAXONOMY

Ornithoctoninae Pocock 1895
Citharognathus Pocock 1895

Citharognathus Pocock 1895:179; Raven 1985:115,116; Smith 1988:104, 105.

Type species.—*Citharognathus hosei* Pocock 1895, by original designation.

Diagnosis.—Differs from *Ornithoctonus* Pocock 1892 and other genera of Ornithoctoninae by: the clypeus less than width of eye group (Fig. 1A), leg IV distinctly longer and thicker than leg I, tibia and metatarsus IV thickest (Fig. 1F), tibia IV wider than femur IV.

Description.—See Pocock (1895) and the description of *Citharognathus tongmianensis* (Zhu et al. 2002).

Distribution.—China, Malaysia.

Remarks.—*Citharognathus*currently contains two species, known only from the female. One species was reported in China.

This genus was erected by Pocock 1895 (from Sarawk of Malaysia, only the female). Pocock described this species in detail and provided illustrations of the carapace, sternum, and leg IV. Zhu et al. (2002) described another species, *Citharognathus tongmianensis* Zhu et al. 2002 (from Ningming County, Guangxi Province, China; female only).

Citharognathus tongmianensis Zhu, Li & Song 2002
Figs. 1, 19

Citharognathus tongmianensis Zhu et al. 2002:371, figs. 1, 2 (holotype and 1 paratype females from Guangxi, China, deposited in MHBU, examined).

Material examined.—♀ (holotype, MHBU-Ar.T0029), 1 ♀(paratype, MHBU-Ar.T0030), CHINA: Guangxi Province, Ningming County, Tongmian Village, 21°46′N, 107°19′E, 15 Jan. 2002, T. H. Li leg. (MHBU).

Diagnosis.—This species resembles *C. hosei* Pocock 1895, but can be distinguished by larger body size; lacking dark stripes on abdomen dorsally; clypeus which is wider than AME diameter; the ALE largest (Fig. 1A); metatarsus III shorter than metatarsus I; scopula of metatarsus III reaches to 1/2 leg length; scopula of metatarsus IV divided by four rows

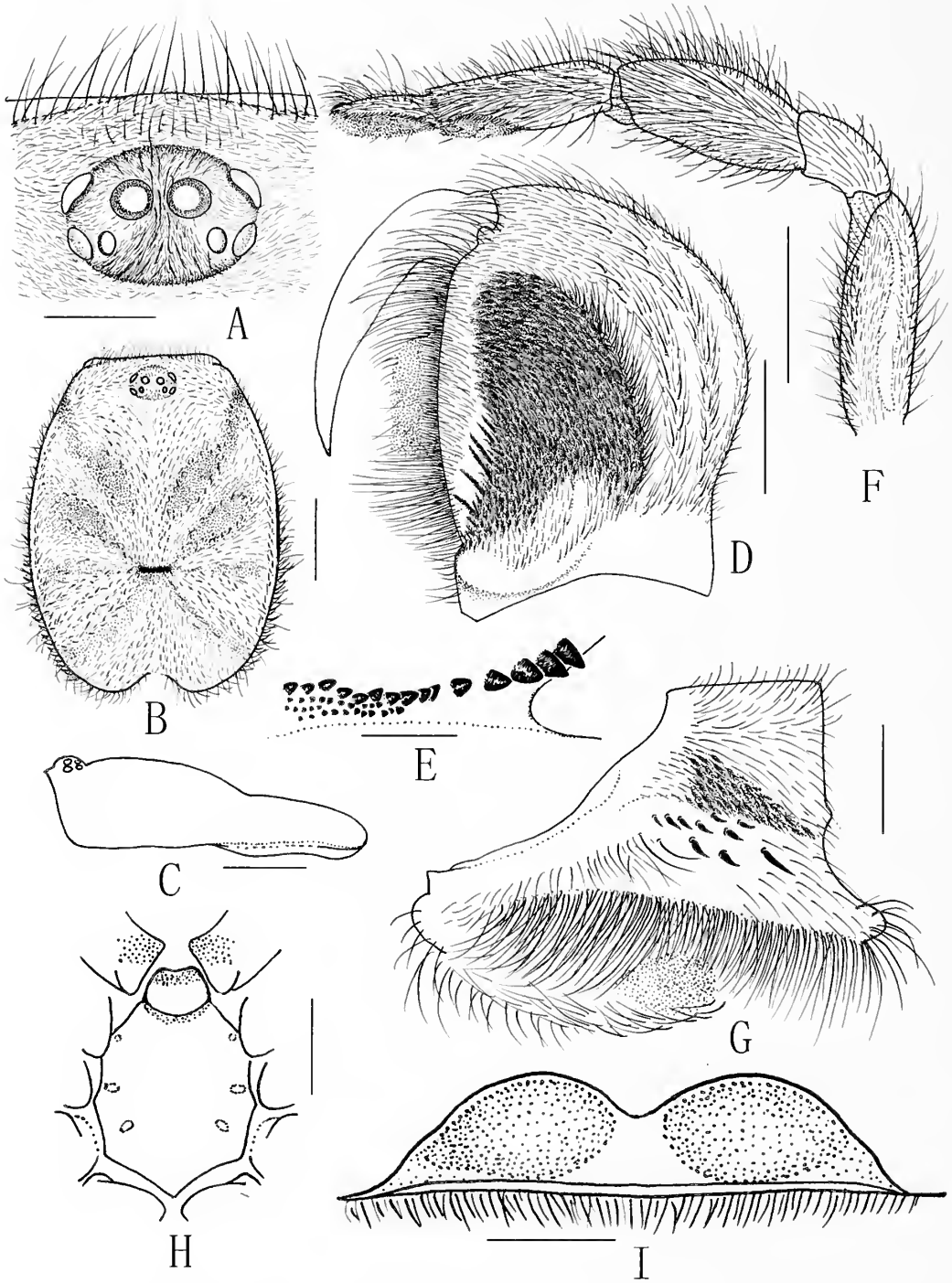

Figure 1.—*Citharognathus tongmianensis* Zhu, Li & Song, 2002. A–I. Holotype female (MHBU-Ar.T0029). A. Eyes, dorsal view; B. Carapace, dorsal view; C. Same, lateral view; D. Left chelicerae, retrolateral view; E. Denitition of left chelicerae; F. Left leg IV, retrolateral view; G. Maxillae, prolateral view; H. Labium and sternum, ventral view; I. Spermathecae, dorsal view. Scale bars: 1 mm (I), 2mm (A, E–G), 5mm (B–D, H).

of setae, reaches to 1/3 leg length; numerous long hairs on retrolateral tibia and metatarsus IV (Fig. 1F).

Redescription.—*Holotype (female):* total length 53.4; cephalothorax 21.4 long, 18.1 wide; abdomen 32.0 long, 23.5 wide. Carapace low, covered with yellowish brown thin hairs and black spinulose hairs (Fig. 1B). Eye tubercle small; eye group 1.57 long, 3.51 wide. ALE 0.90, AME 0.72, PLE 0.63, PME 0.54; ALE–AME 0.27, AME–AME 0.45, PLE–PME 0.10, PME–PME 1.44; MOA 1.39 long, front width 1.80, back width 2.14; clypeus 1.26 wide. Outer cheliceral face with scopulae; inner margin with 15 teeth and some basal denticles. Maxillae with ca 150 ventral cuspules at base of inner angle, anterior surface with three rows of 10 horizontal spines and a group of plumose hairs (Fig. 1G); outer surface of trochanter of palp with plumose hairs. Anterior border of labium slightly concave, with ca. 144 cuspules (Fig. 1H). Leg IV longest and

thickest, with its tibia and metatarsus with numerous long hairs retrolaterally (Fig. 1F). All tarsi with 2 claws, with 0-2 denticles, but with a third claw on tarsus IV. Metatarsus I with scopula to 4/5, undivided; metatarsus II with scopula to 2/3, undivided; metatarsus III with scopula to 1/2, undivided; scopula of metatarsus IV reaches to 1/3, divided by four rows of setae. Leg measurements: I 54.63 (17.73 + 9.90 + 11.34 + 9.27 + 6.39); II 45.72 (13.50 + 8.55 + 9.00 + 8.64 + 6.03); III 41.76 (12.24 + 7.92 + 7.29 + 8.64 + 5. 67); IV 64.53 (17.73 + 10.17 + 15.30 + 14.94 + 6.39). Leg formula: 4123. Abdomen spinulose, covered with grayish yellow short and thin hairs. Spermatheca fused and breast-shaped (Fig. 1I).

Male: unknown.

Distribution.—China (Guangxi).

Haplopelma Simon 1892

Haplopelma Simon 1892:151; Simon 1903:946; Raven 1985:116; Smith 1996:104; Schmidt 1998:2, 2005:3; von Wirth & Striffler 2005:2.

Melopoeus Pocock 1895:179.

Type species.—*Selenocosmia doriae* Thorell 1890, by original designation.

Diagnosis.—Can be distinguished from all genera of Ornithoctoninae except *Ornithoctonus* by the high, distinctly arched caput, small ocular tubercle and wide clypeus (Figs. 2A, 3A). The fovea is straight or slightly procurved and the legs are long; males with leg I being slightly thicker than leg IV. *Ornithoctonus* from Burma and South China closely resemble *Haplopelma*, but can be readily identified by the short stout legs of equal thickness. The carapace is elevated and the clypeus wide (Raven 1985; Smith 1996).

Description.—Medium to large sized spiders. Carapace black brown, hirsute. Eight eyes on distinct tubercle. Clypeus wide. Fovea deep, procurved. Outer cheliceral face with many long and slightly curved plumose hairs (Fig. 3F), and maxillae with recumbent thorns prolaterally (Fig. 2B); together forming a stridulating organ. Inner margin of chelicerae with row of strong teeth and some denticles. Distal labium and prolateral maxillae with cuspules. Distal spur on prolateral tibia I of male. Tarsus of each leg with tarsal organ distally. Ordinary and claviform trichobothria present on tarsi of palp and legs. Leg formula: 1423. Palpal bulb pear-like, embolus wide, curved. Spermatheca M-shaped with obvious central hollow or hemisphered.

Distribution.—Southeast Asia (China, Burma, Thailand, Cambodia, Malaysia, Singapore, Vietnam) and Borneo.

Remarks.—The spiders are usually found in small colonies at the base of trees or among the roots of bamboo clumps. The retreat consists of a tube of varying length with a distinct silk funnel. The funnel and outlying web often contain leaves and detritus, making the funnel difficult to locate.

Genus *Haplopelma* currently contains 11 species, distributed in Southeast Asia, two species are reported from China (Platnick 2008).

KEY TO CHINESE SPECIES OF *HAPLOPELMA*

1. Body dark black brown; 24–28 longer thorns on prolateral maxillae (Fig. 2B); length of spermatheca more than half of its width (Fig. 2D); embolus strongly curved (Fig. 2E–G) ..... *Haplopelma hainanum*
– Body dark yellow brown; 19–20 short, small thorns on prolateral maxillae (Fig. 3E); the length of spermatheca about one-fifth of its width (Fig. 3C, D); embolus slightly curved (Fig. 3I–K) ..... *Haplopelma schmidti*

Haplopelma hainanum (Liang et al. 1999)
Figs. 2, 10–12, 19

Selenocosmia hainana Liang et al. 1999:300, figs. 1–4. (holotype female from Hainan Province, deposited in HNU, not examined); Chen et al. 2004. (males from Hainan Province).

Ornithoctonus hainana: Zhu et al. 2001:1, figs. 1–7 (first description of both male and female)

Haplopelma hainanum: Schmidt 2003:250, figs. 815–817; von Wirth & Striffler 2005:17.

Material examined.—2 ♀♀, MHBU-Ar.T0018–0019; 2 ♂♂, MHBU-Ar.T0020–0021, CHINA: Hainan Province, Tongza City, 18°46′N, 109°31′E, May 1999, T. H. Li leg. (MHBU).

Diagnosis.—Males of this species resemble *H. schmidti* von Wirth 1991 in the shape of palp, but can be distinguished by the dark black brown body (Fig. 10), 24–28 longer thorns on prolateral maxillae (Fig. 2B), the spermatheca with length more than half of its width (Fig. 2D), and the strongly curved embolus (Fig. 2E–G).

Redescription.—*Female:* Total length (including chelicerae) 59.05, cephalothorax 24.75 long, 22.60 wide; abdomen 24.30 long, 15.75 wide. Carapace black brown. Eye group 1.62 long, 3.87 wide. MOA 1.35 long, front width 1.89, back width 2.34 (Fig. 2A). Eye sizes: ALE 0.90, AME 0.72, PLE 0.72, PME 0.45. Clypeus 2.25 wide. Fovea deep, slightly procurved. Chelicerae 7.65 long, outer cheliceral face with short scopula, lower surface with 9 long and slightly curved plumose hairs. Inner margin of chelicerae with 15 strong teeth and 4 denticles. Labium wider than long, with ca. 83 cuspules. Maxillae with 28 recumbent thorns in four rows prolaterally (Fig. 2B), with ca 149 cuspules ventrally. Sternum red-brown with 3 pairs of sigilla. Palpal tibia with many long, brown, thin hairs. Legs with long and short hairs. Tarsi I–IV with scopulae full. Tarsi with 2 claws, without denticles. Metatarsi I, II with scopulae full, metatarsus III with scopula to 2/3, scopula of metatarsus IV reaches to 1/3, divided by two rows of setae. Tibiae I–IV with 2 ventral spines distally. Metatarsus I with 1 ventral spine distally, metatarsus II without spine and metatarsus III with 2 ventral spines, 2 prolateral spines and 1 retrolateral spine distally. Only the scopula of metatarsus IV divided. Palp and legs measurements: Palp 41.94 (14.22 + 8.91 + 10.89 + 7.92), I 67.05 (20.25 + 11.88 + 14.67 + 12.78 + 7.47), II 58.86 (17.46 + 10.53 + 12.51 + 11.97 + 6.39), III 50.85 (14.04 + 9.27 + 9.99 + 12.06 + 5.49), IV 61.61 (19.08 + 10.08 + 13.59 + 16.29 + 6.57). Leg formula: 1423. Abdomen is dark brown, with six black transverse stripes and one black longitudinal stripe in the middle of dorsum. Spermatheca is M-shaped, length almost half of its width (Fig. 2D). PMS 2.25 long, 1.08 wide; PLS 9.99 (3.51 + 2.88 + 3.60).

Male: Total length 33.93, cephalothorax 17.37 long, 16.20 wide; abdomen 16.56 long, 11.34 wide. Eye group 1.45 long,

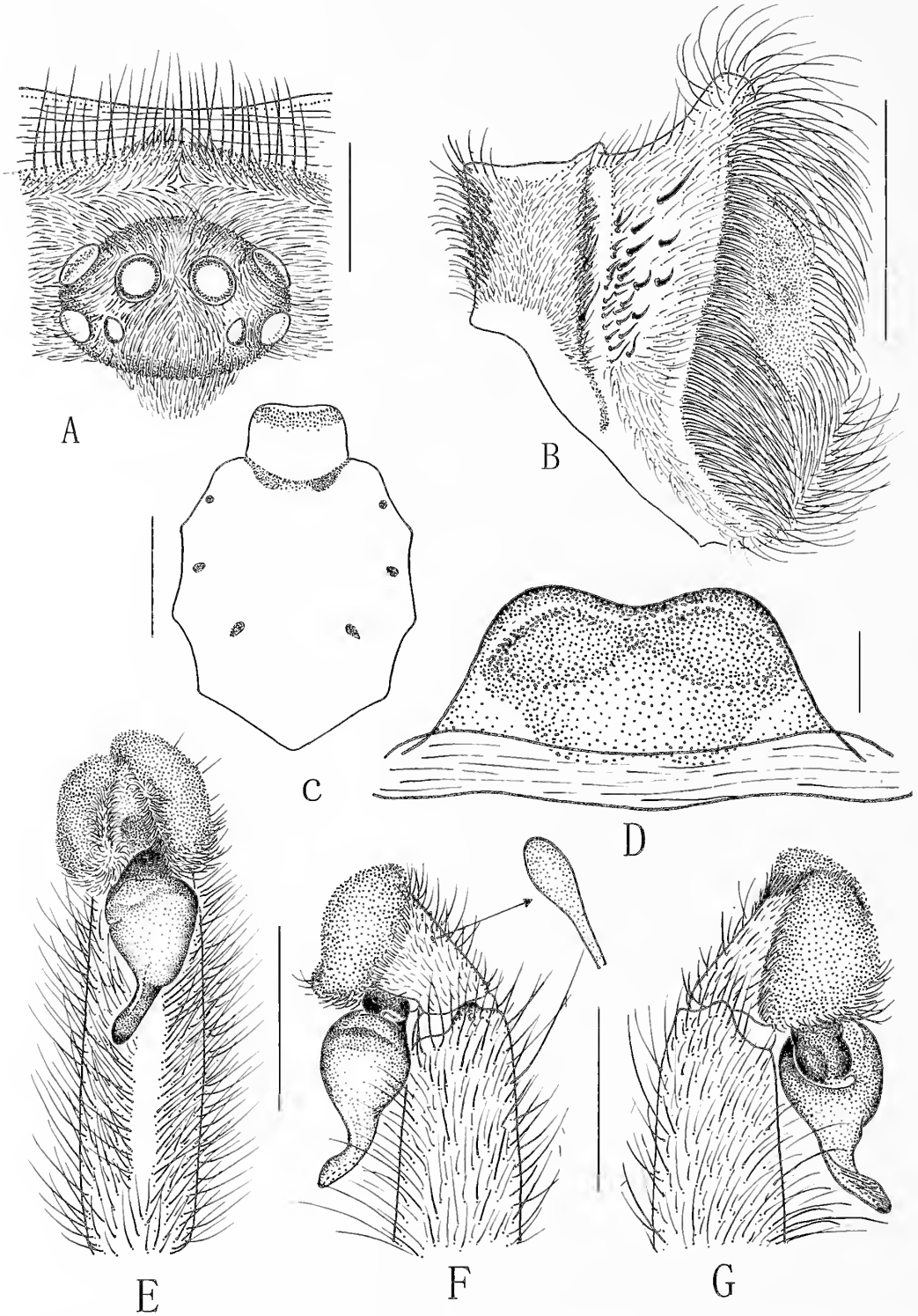

Figure 2.—*Haplopelma hainanum* (Liang et al., 1999). A–D. Female (MHBU-Ar.T0018). A. Eyes, dorsal view; B. Maxillae, prolateral view; C. Labium and sternum, ventral view; D. Spermathecae, dorsal view; E–G. Male (MHBU-Ar.T0021). E. Left pedipalp, ventral view; F. Same, retrolateral view; G. Same, prolateral view. Scale bars: 1 mm (D), 2mm (A), 5 mm (B–C, E–G).

3.21 wide. MOA 1.34 long, front width 1.61, back width 2.09. Eye sizes and interdistances: ALE 0.75, AME 0.70, PLE 0.59, PME 0.32; ALE–AME 0.38, AME–AME 0.38, PLE–PME 0.11, PME–PME 1.50. Clypeus 0.80 wide. Chelicerae 7.80 long, outer cheliceral face with 7 long and slightly curved plumose hairs on lower surface. Inner margin of chelicerae with 16 strong teeth and 1 denticle. Labium wider than long, with ca 97 cuspules. Maxillae with 24 recumbent thorns in about three lines above the suture prolaterally, plumose hairs and a row of long spines present below the suture; with ca 155 cuspules ventrally. Tibiae I–III with 2 ventral spines distally, tibia IV with 1 ventral spine, metatarsus I with 1 ventral spine distally, metatarsus II with 2 spines and 1 prolateral spine, metatarsus III with 3 ventral spines, 1 dorsal spine and 2

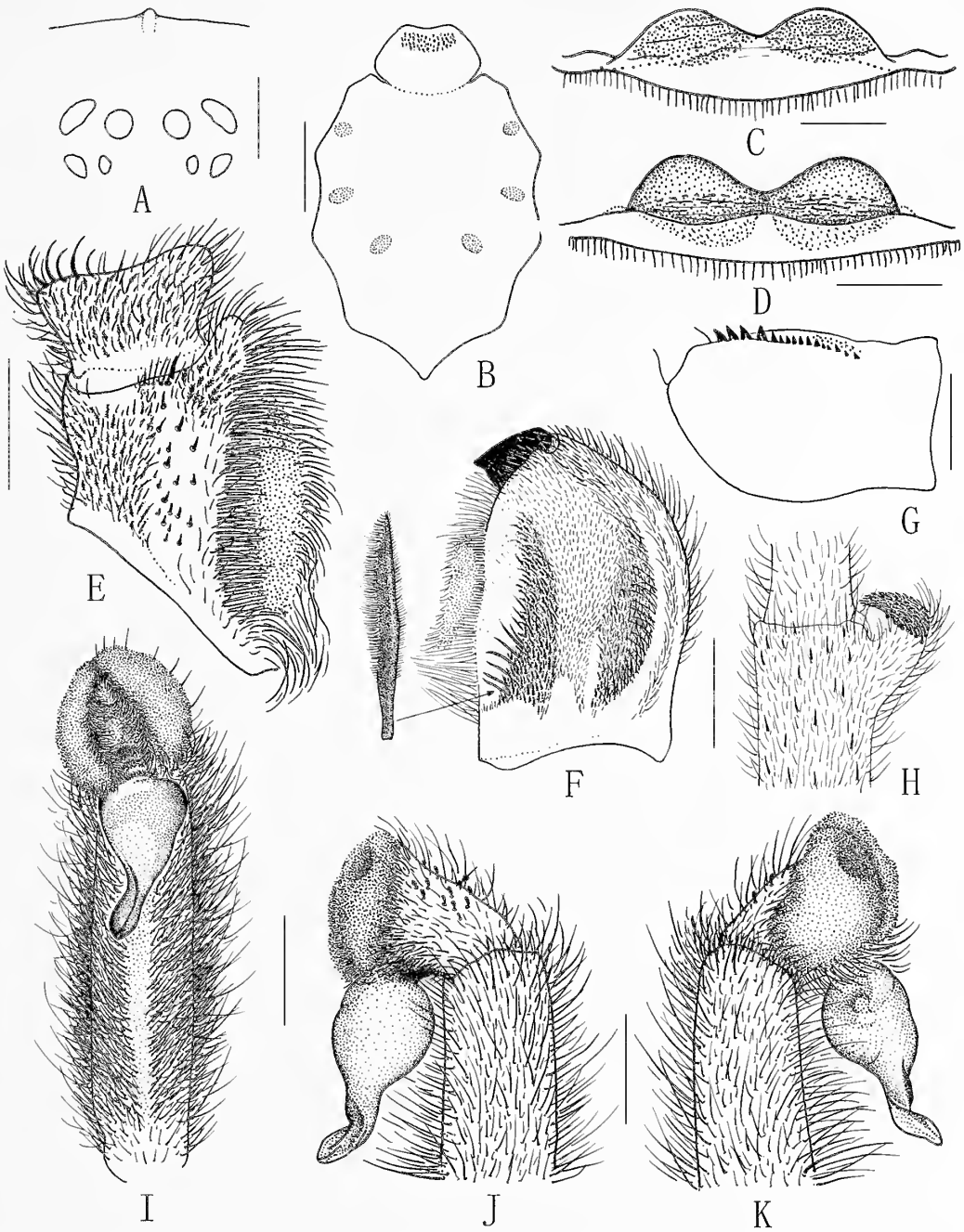

Figure 3.—*Haplopelma schmidti* von Wirth, 1991. A–D. Female (MHBU-Ar.T0003). A. Eyes, dorsal view; B. Labium and sternum, ventral view; C, D. Spermathecae, dorsal view; E–K. Male (MHBU-Ar.T0011). E. Maxillae, prolateral view; F. Left chelicerae, retrolateral view; G. Left chelicerae, prolateral view; H. Leg I, distal end of tibia; I. Left pedipalp, ventral view; J. Same, retrolateral view; K. Same, prolateral view. Scale bars: 2 mm (A, C, D), 5 mm (B, E–K).

prolateral spines. Tibia I with 1 prolateral spur distally. Palp and leg measurements: Palp 32.04 (11.16 + 6.57 + 9.81 + 4.50), I 59.31 (16.11 + 8.64 + 14.13 + 13.05 + 7.38), II 55.08 (15.12 + 8.55 + 12.06 + 12.24 + 7.11), III 47.34 (13.59 + 7.38 + 9.27 + 10.98 + 6.12), IV 60.57 (16.56 + 8.37 + 13.59 + 15.57 + 6.48). Leg formula: 4123. Tarsus of palp with more than 40 claviform trichobothria dorsally. Palpal bulb pear-like, embolus wide and curved (Fig. 2E–G).

Distribution.—China (Hainan Island).

Natural history.—Its habitat lies in steep, south facing mountain slopes, between 75°–85° from horizontal, always in an underground burrow made in the sand and earth, with a nearly round opening. Opening and burrow lined with white silk. During daytime they hide in the burrow and at night come out to catch prey, mainly large insects, often using radiating silk alarm lines (Figs. 11, 12).

Haplopelma schmidti von Wirth 1991
Figs. 3, 13–16, 19

Haplopelma schmidti von Wirth 1991:7, figs. 1–11 (holotype female from North-Vietnam, deposited in SMF, not examined); Schmidt 1993:122, figs. 386, 393; Schmidt

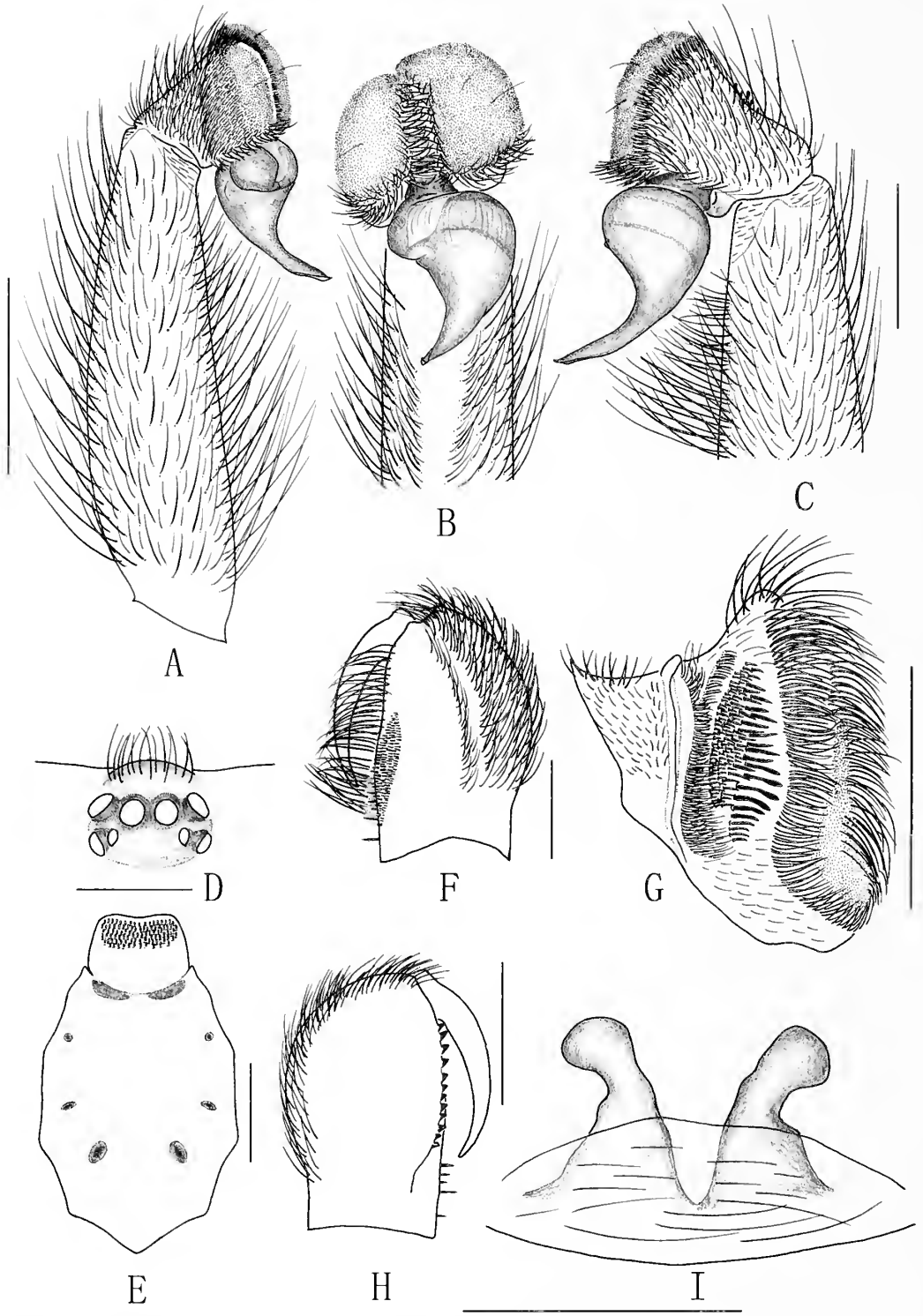

Figure 4.—*Chilobrachys guangxiensis* (Yin & Tan, 2000). A–H. Male (MHBU-Ar.T0025). A. Left pedipalp, prolateral view; B. Same, ventral view; C. Same, retrolateral view; D. Eyes, dorsal view; E. Labium and sternum, ventral view; F. Left chelicerae, retrolateral view; G. Maxillae, prolateral view; H. Left chelicerae, prolateral view; I. Female (MHBU-Ar.T0022): spermathecae, dorsal view. Scale bars: 3 mm (B–D, G, I), 5 mm (A, E, F, H).

2003:251, figs. 822–825; Peters 1999:11, figs. 2, 3; Peters 2000:19, fig. 35; von Wirth & Striffler 2005:23.

Selenocosmia huwena Wang et al. 1993:72, figs. 1–6 (holotype female and 7 paratypes females from Guangxi, China, deposited in HNU, not examined); Yin & Bao 1995:131, figs. 1–9 (male); Song et al. 1999:40, figs. 17 N–P. First synonymized by Schmidt 2000.

Ornithoctonus huwena: Zhu & Song 2000:54, figs. 1–16; Chen et al. 2003:70, fig. 8.

Haplopelma huwenum: Schmidt 2000:77, 2003:251.

Material examined.—10 ♀♀, MHBU-Ar.T0001–0010; 4 ♂♂, MHBU-Ar.T0011–0014, CHINA: Guangxi Province, Ningming County, 22°08′N, 107°04′E, Jun. 1999, M.S. Zhu and T.H. Li leg. (MHBU); 2♀♀, MHBU-Ar.T00150016; 1♂, MHBU-Ar.T0017, Guangxi Province, Pingxiang City, 22°06′N, 106°45′E, 26 Dec. 2004, M.S. Zhu leg. (MHBU).

Diagnosis.—This species resembles *Haplopelma hainanum* (Liang et al. 1999), but it can be distinguished by the dark yellow brown body (Figs.13, 14); 19–20 short, small recumbent thorns on prolateral maxillae, by the length of spermatheca about one-fifth of its width (Fig. 3C, D), and by the slightly curved embolus (Fig. 3I–K).

Redescription.—*Female:* Total length (including chelicerae) 53.00–85.15. Body length 67.14, cephalothorax 32.14 long, 28.92 wide; abdomen 35.10 long, 27.10 wide. Carapace dark yellow brown, with yellow brown long and short hairs. Carapace low, caput slightly arched. Eye tubercle low, eye group 1.77 long, 3.75 wide (Fig. 3A). MOA 1.45 long, front width 1.86, back width 2.30. Eye sizes and interdistances: ALE 1.02, AME 0.75, PLE 0.75, PME 0.27; ALE–AME 0.32, AME–AME 0.32, PLE–PME 0.11, PME–PME 1.45. Clypeus 1.61 wide. Fovea deep, procurved. Chelicerae 7.92 long, outer cheliceral face with short scopula, lower surface to central with plumose hairs, marginal row longest and strongest. Inner margin of chelicerae with 21 strong teeth. Labium wider than long, with ca. 82 cuspules. Maxillae with ca. 180 cuspules ventrally and with 19 prolateral recumbent thorns and plumose hairs on outer face of chelicerae together forming a stridulating organ. Tarsi with 2 claws, without denticles. Tarsus with paddle setae dorsally. Prolateral and retrolateral coxa I, prolateral trochanter I with plumose hairs. Metatarsi I–III with seopulae full, metatarsus IV with scopula reaehes to 1/3. Tibiae I and IV with 2 ventral spines distally, tibia II with 2 prolateral spines distally, tibia III without spines. Metatarsus I and IV with spines, metatarsus II with 1 retrolateral spine, 2 ventral spines distally and 3 prolateral spines distally, metatarsus III with 3 ventral spines distally, 1 prolateral spine and 2 dorsal spines. Legs measurements: I 69.20 (21.00 + 12.00 + 15.00 + 13.00 + 8.20), II 63.40 (19.50 + 10.90 + 13.00 + 12.90 + 7.10), III 53.80 (16.50 + 9.50 + 9.80 + 12.10 + 5.90), IV 67.70 (21.10 + 10.20 + 13.90 + 16.60 + 6.90). Leg formula: 1423. Abdomen yellow brown, with blaek transverse stripes and one black longitudinal stripe in the middle of dorsum. Spermatheca M-shaped with a central hollow (Fig. 3C, D).

Male: Total length (including chelicerae) 37.70–44.00. Body length 37.70, cephalothorax 19.16 long, 16.19 wide; abdomen 18.54 long, 13.72 wide. Eye group 1.39 long, 2.89 wide. MOA 1.23 long, front width 1.55, back width 2.04. Eye sizes and interdistances: ALE 0.80, AME 0.64, PLE 0.64, PME 0.27; ALE–AME 0.21, AME–AME 0.32, PLE–PME 0.05, PME–PME 1.34. Clypeus 1.35 wide. Stridulating setae on chelicerae and maxillae resembles (Fig. 3F) that of female. Labium wider than long, with ca. 87 cuspules. Maxillae with ca. 158 cuspules ventrally and with 20 recumbent thorns on prolateral (Fig. 3E). Tibia I with 1 prolateral spur distally. (Fig. 3H). Tibiae I–IV with 2 ventral spines distally, metatarsi I and II with 1 dorsal spine and 2 ventral spines distally, metatarsi III and IV without dorsal spine, with 2 ventral spines and 1 prolateral spine, and 1 retrolateral spine distally. Legs measurements: I 67.60 (18.80 + 9.70 + 15.10 + 15.50 + 8.50), II 60.30 (17.10 + 8.60 + 13.20 + 13.90 + 7.50), III 51.93 (14.83 + 7.80 + 12.20 + 12.90 + 6.20), IV 66.07 (18.17 + 8.10 + 15.10 + 17.80 + 6.90). Leg formula: 1423. Tarsus of palp with bands of claviform trichobothria dorsally. Palpal bulb pear-like, embolus wide, curved (Fig. 3I–K).

Distribution.—China (Guangxi), Vietnam.

Remarks.—This species was originally described by von Wirth (1991b) based on one female specimen from Vietnam. Wang et al. (1993) described *Selenocosmia huwena* Wang, Peng & Xie, 1993 based on specimens from Guangxi (holotype, female) and Yunnan (allotype, male), China. Yin & Bao (1995) proposed that the male and female of *S. huwena* Wang, Peng & Xie 1993 were incorrectly matched and supplemented and redescribed the male specimens of this species. *Selenocosmia huwena* was transferred to *Ornithoctonus* by Zhu & Song (2000). Schmidt (2000) synonymized *S. huwena* Wang, Peng & Xie 1993 with *Haplopelma schmidti* von Wirth 1991 according to similar characters. In examining additional material, we found that certain specimens of the genus *Haplopelma* that had been collected from the nearby region of Guangxi Province (Pingxiang to Youyiguan) were the same as those collected in Vietnam, *H. huwenum.* We agree with Schmidt that *H. huwenum* is a junior synonym of *H. schmidti.*

Natural history.—Its habitat lies in steep, south facing mountain slopes, between 60°–85° from horizontal, always in an under ground burrow made in the yellow sand and earth, with a nearly round opening but possibly with a bit of grass around the opening. Opening and burrow lined with white silk. During the daytime they hide in the burrow and at night come out to catch prey, mainly large insects, often using radiating silk alarm lines (Fig. 15, 16).

Selenocosmiinae Simon 1889

Chilobrachys Karsch 1891

Chilobrachys Karsch 1891:271; Pocock 1900:195; Gravely 1915:285; Raven 1985:118; Smith 1986:115.
Musagetes Pocock 1895:172.

Type species.—*Chilobrachys nitelinus* Karsch 1891, by original designation.

Diagnosis.—Anterior eyes in a nearly straight line. Stridulating organ consists of short spines on the chelicerae (Fig. 3F) and a single or double row of paddle hairs, overlapped by a fringe of hairs on the maxillae (Fig. 4G). The bacilliform hairs are not accompanied by tubercles. Legs with narrower scopulae at the tip of metatarsus. Palpal organ of male ending in a long and slender or blade-like spine (Raven 1985; Smith 1986).

Description.—Medium to large spiders, Eye tubercle low, clypeus wide. Fovea procurved. Outer cheliceral face with small area of peg-like setae. Inner margin of chelicerae with row of strong teeth and some small teeth. Distal labium and prolateral maxillae with cuspules. Maxillae with setae arranged like combs prolaterally, the lowest three rows biggest, which may be paddle-shaped, bacilliform-shaped, or lance-shaped. Sternum red-brown with 3 pairs of sigilla. PLS with apical segment digitiform. Palpal bulb pear-like, embolus thin, long, with small distal groove. Tarsi of legs with 2 or 3 claws. One pair of spermatheca.

Distribution.—Southeast Asia, India.

Remarks.—*Chilobrachys* was described for a female specimen from Sri Lanka. Pocock (1900) found the male specimen of the type species and redescribed it in detail. He also considered the genus *Musagetes* Pocock 1985 as a junior synonym of *Chilobrachys*.

Genus *Chilobrachys* currently contains 23 species. Three species are reported from China: *C. liboensis* sp. nov., *C. guangxiensis* (Yin & Tan 2000) is newly transferred here from the genus *Plesiophrictus*, *C. jingzhao* Zhu, Song & Li 2001 is considered a junior synonym of *C. guangxiensis* (Yin & Tan 2000).

KEY TO CHINESE SPECIES OF *CHILOBRACHYS*

1. Embolus short, wide (Fig. 4A–C), with length similar to basal palpal bulb, fewer paddle-shaped setae on prolateral maxillae (Fig. 4G) ..... *C. guangxiensis*
– Embolus long, thin (Fig. 5A), with length much longer than basal palpal bulb, many paddle-shaped setae on prolateral maxillae ... 2
2. ALE larger than AME (Fig. 5D), embolus with short groove at top (Figs. 5A–C), tarsus IV with 3 claws, no denticles on paired claws, length of cephalothorax is shorter than metatarsus IV ..... *C. liboensis* sp. nov.
– ALE equal to AME, embolus with longer groove at distal half, tarsus IV with 2 claws, with 1 denticle on each claw, length of cephalothorax equal to metatarsus IV ..... *C. hubei*

Chilobrachys guangxiensis (Yin & Tan 2000) comb. nov
Figs. 4, 17, 18, 19

Plesiophrictus guangxiensis Yin & Tan 2000:152, figs. 1–10 (holotype female and 2 paratype females from Guangxi, China, deposited in HNU, not examined); Chen et al. 2004:606, figs. 1–4 (male); Chen et al. 2004:665, figs. 12–14 (male, not examined).

Chilobrachys jingzhao Zhu et al. 2001:3, figs. 8–13 (female holotype and 1 female paratype from Ledong County, Hainan, China, deposited in MBHU, examined). New synonymy.

Material examined.—CHINA: 2♀♀ (*Chilobrachys jingzhao*, holotype female, MHBU-Ar.T0022–0023 and 1 paratype female, MHBU-Ar.T0024, MHBU); 2♂♂, *Chilobrachys jingzhao*, MHBU-Ar.T0025–0026; 1♀, *Chilobrachys jingzhao*, MHBU-Ar.T0027, Hainan Province, Ledong County, 18°70′N, 109°10′E, 27 Aug. 2003, M.S. Zhu leg. (MBHU); 1♀, *Chilobrachys jingzhao*, MHBU-Ar.T0028, Hainan Province, Nan-dao Farm, Dec. 2003, M.S. Zhu leg (MBHU).

Diagnosis.—Females are similar to *C. huahini* Schmidt & Huber 1996 in the shape of the spermathecae, but differ from females of the latter by leg IV longer than leg I; the peg-like setae on lower surface of outer chelicerae occupying a larger area (Fig. 4F); and lyra-shaped setae on maxillae arranged like narrow, long combs (Fig. 4G); inner margins of spermatheca lacking concavity (Fig. 4I). Males are similar to *C. hubei* Song & Zhao 1988, but can be distinguished by the different shape of the palpal bulb (Fig. 4A–C).

Redescription.—*Male:* Total length (including chelicerae) 55.00–59.00. Body length 59.00, cephalothorax 25.00 long, 23.00 wide; abdomen 27.00 long, 18.00 wide. Carapace red-brown, with gray hairs (Fig. 17). Eye group 1.88 long, 3.32 wide (Fig. 4D). Anterior eye row slightly procurved; posterior eye row recurved. MOA 1.34 long, front width 0.75, back width 1.07. Eye sizes and interdistances: ALE 0.80, AME 0.70, PLE 0.70, PME 0.43; ALE–AME 0.27, AME–AME 0.32, PLE–PME 0.75, PME–PME 1.34. Clypeus 0.80 wide. Fovea procurved. Chelicerae black-brown, 10.00 long, an area of peg-like setae near lower surface, inner margin with 12 strong and some small teeth. Labium wider than long, with ca 959 cuspules. Maxillae with many setae arranged like combs prolaterally; lowest row long paddle-shaped, bacilliform-shaped, or lance-shaped; with ca 416 cuspules ventrally. Sternum red-brown with 3 pairs of sigilla (Fig. 4E). Palpal bulb pear-like, embolus straight, long, thin with short distal groove, sector-like at top, the palpal bulb and embolus 4.33 long. Legs with long and short hairs. Tarsi and metatarsi I, II with scopulae full and undivided, tarsus III with scopula full and undivided, metatarsus III with scopula reaches to 4/5, tarsus IV scopulae full and divided by rows of bristles, scopula of metatarsus IV sparse and only reaches 1/2 and divided. Tarsi I– III with 2 claws, without denticles, tarsus IV with third claw, no denticles on paired claws. Palp and leg measurements: Palp 38.00 (14.00 + 8.00 + 12.00 + 4.00), I 73.00 (21.00 + 11.00 + 17.00 + 14.00 + 10.00), II 67.00 (19.00 + 10.00 + 14.00 + 14.00 + 10.00), III 60.00 (17.00 + 8.00 + 12.00 + 14.00 + 9.00), IV 78.00 (21.00 + 10.00 + 18.00 + 20.00 + 9.00). Leg formula: 4123. Abdomen oval, fawn, with long brown hairs and thick short fawn hairs. PMS 2.85 long, 1.16 wide; PLS 14.00 long (5.00 + 4.00 + 5.00), PMS–PMS 0.84.

Female: Total length (including chelicerae) 64.34, cephalothorax 25.20 long, 22.68 wide; abdomen 31.13 long, 23.11 wide. Eye group 1.71 long, 3.60 wide. MOA 1.53 long, front width 1.80, back width 2.70. Eye interdistances: ALE–AME 0.27, AME–AME 0.54, PLE–PME 0.09, PME–PME 1.62. Clypeus 1.08 wide. Chelicerae black brown, 8.01 long; inner margin with 14 strong teeth and 5 small teeth, with some small teeth at base. Labium, maxillae and sternum like those of male, labium with ca 1032 cuspules, maxillae with ca 490 cuspules ventrally. Palp and legs with many long brown and thin hairs. Tarsi and metatarsi I, II with full scopulae and undivided, tarsus III with scopula full, metatarsus III with scopula reaches to 4/5, tarsus IV scopulae full and divided by rows of bristles, scopula of metatarsus IV sparse and only reaches to 3/5. Tarsi I–III with 2 claws without denticles; tarsus IV with 3 claws; paired claws with two tiny denticles or none. Palp and legs measurements: palp 41.39 (14.85 + 9.00 + 9.81 + 7.65), I 64.71 (19.26 + 11.88 + 13.59 + 12.42 + 7.20), II 59.04 (17.37 + 10.62 + 12.15 + 11.70 + 7.20), III 50.94 (14.76 + 8.55 + 9.72 + 11.16 + 6. 75), IV 69.40 (19.80 + 10.35 + 13.95 + 17.82 + 7.38). Leg formula: 4123. PMS 3.60 long, 1.35 wide; PLS 17.46 long (6.30 + 4.86 + 6.30), PMS–PMS 1.35. One pair of spermathecae, wide at base and thins upwards gradually, distal part swollen and bending to one side (Fig. 4I).

Distribution.—China (Hainan).

Natural history.—found in ground burrow on mountain slopes (Fig. 18).

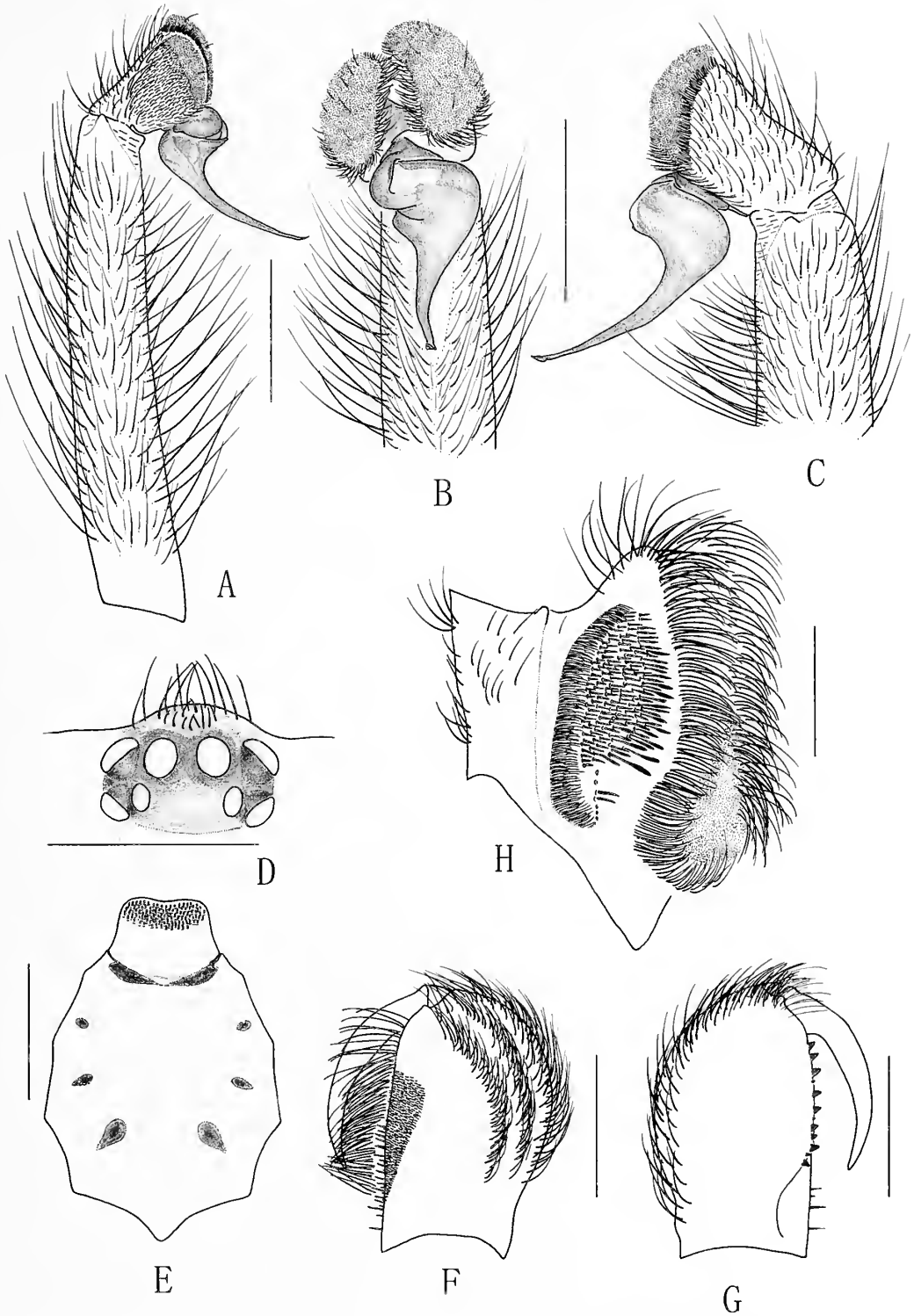

Figure 5.—*Chilobrachys liboensis* sp. nov. A–H. Holotype male (MHBU-Ar.T0031). A. Left pedipalp, prolateral view; B. Same, ventral view; C. Same, retrolateral view; D. Eyes, dorsal view; E. Labium and sternum, ventral view; F. Left chelicerae, retrolateral view; G. Maxillae, prolateral view; H. Left chelicerae, prolateral view. Scale bars: 1 mm (H), 3 mm (A–G).

Remarks.—This species was originally described by Yin & Tan (2000) for females from Rong County, Guangxi Province, China, and placed in genus *Plesiophrictus*. Chen et al. (2004) described the males from Wuzhishan City, Hainan Province; at the same time they also pointed out that the type locality (originally recorded from Guangxi Province by Yin & Tan 2000) is wrong. In fact, the holotype female and 2 paratype females were collected from Hainan Province.

The characters of this species are very different from the genus *Plesiophrictus* described by Raven (1985). We transferred *Plesiophrictus guangxiensis* Yin & Tan 2000 herein to genus *Chilobrachys* according to the horizontal spines of the

maxillae and the setae of the cheliceral stridulating organ as mentioned in Chen et al. 2004 (cf. figs: 23–26).

By examining the types of *C. jingzhao* Zhu, Song & Li 2001 from Hainan Province, we find that *C. jingzhao* is a synonym of *C. guangxiensis* because: (1) the locality of both the types are from Hainan Province (an island); (2) the body sizes are elose; (3) the genitalic illustrations of *C. guangxiensis* given by Yin & Tan (2000, cf. fig. I) and Chen et al. (2004, cf. figs. 1–4) correspond to those given by Zhu et al. (2001).

Chilobrachys hubei Song & Zhao 1988

Chilobrachys hubei Song & Zhao 1988:1, figs. 1, 2 (holotype male and paratype male from Hubei, China, deposited in IZB, lost and not examined); Song et al. 1999:40, figs. 17L, M.

Diagnosis.—This species resembles *C. andersonii* (Pocock 1895), but can be distinguished from the latter by the carapace longer than metatarsus IV and shorter than the total length of patella and tibia III; embolus with longer groove at distal half (Song & Zhao 1988).

Distribution.—China: Hubei.

Remarks.—This species was originally described for two male specimens from Badong County, Hubei Province, China. The type specimens were lost and no new materials have been collected.

Chilobrachys liboensis sp. nov.
Figs. 5, 19

Type material.—Holotype ♂, MHBU-Ar.T0031, CHINA: Guizhou Province, Libo County, 25°24′N, 107°52′E, Weng'ang Village, 23 Sept. 2000, H.M. Chen leg.(MBHU).

Etymology.—The specific name refers to the type locality.

Diagnosis.—The new species resembles *C. hubei* Song & Zhao 1988, but the ALE of this new species are larger than AME (Fig. 5D), tarsus IV with 3 claws and paired claws without denticles, the length of carapace is shorter than metatarsus IV, embolus with short groove at top (Fig. 5C); whereas in *C. hubei*, the ALE is equal to AME, the tarsus IV without third claw and paired claws with 1 small denticle respectively, and the length of carapace equal to metatarsus IV, embolus with longer groove.

Description.—*Male (holotype):* Total length (including chelicerae) 38.00, cephalothorax 15.00 long, 13.50 wide; abdomen 18.50 long, 12.00 wide. Carapace low, dark red-brown, with gray hairs. Eye group 1.29 long, 2.68 wide (Fig. 5D). Anterior eyes row slightly procurved and posterior eye row recurved from above. MOA 1.13 long, front width 1.34, back width 1.71. Eye sizes and interdistances: ALE 0.70, AME 0.54, PLE 0.59, PME 0.48; ALE–AME 0.16, AME–AME 0.27, PLE–PME 0.11, PME–PME 1.02. Clypeus 0.43 wide. Fovea transverse, procurved. Chelicerae red-brown, 6.00 long; inner margin with 12 strong and 3 small teeth, outer cheliceral face with rows of short setae (Fig. 5F). Labium wider than long, with ca 442 cuspules. Maxillae with many setae arranged as a comb prolaterally; the lowest row longest with paddle-shaped, bacilliform-shaped, or lance-shaped setae (Fig. 5H); with ca 366 cuspules ventrally. Sternum red-brown with 3 pairs of sigilla. Palpal tibia with many long brown and thin hairs. Palpal bulb pear-like, embolus straight, thin, long, with short groove at top (Fig. A–C), the palpal bulb and embolus 4.33 long. Legs with long and short hairs. Tarsi I, II, III and metatarsi I, II with scopula full, undivided, metatarsus III with scopula reaches to half, undivided, tarsus IV scopula full and divided by rows of bristles, scopula of metatarsus IV sparse and only reaches to one sixth. Metatari III and IV with ventral spines distally. Tarsi I–III with 2 claws without denticles, tarsus IV with 3 claws, paired claws without denticles. Palp and legs measurements: Palp 36.30 (14.00 + 7.00 + 11.50 + 3.80, I 61.50 (17.00 + 8.00 + 14.00 + 12.50 + 10.00); II 53.5 (15.00 + 7.50 + 12.00 + 10.50 + 8.50), III 50.00 (13.00 + 6.00 + 11.00 + 11.50 + 8.50), IV 60.5 (16.00 + 6.00 + 14.50 + 15.50 + 8.50). Leg formula: 1423. Abdomen oval and fawn, with long brown hairs and thick short fawn hairs. PMS 2.11 long, 0.63 wide; PLS 9.81 long (3.48 + 2.11 + 4.22), PMS–PMS 0.84.

Female: Unknown.

Distribution.—China (Guizhou).

Selenocosmia Ausserer 1871

Selenocosmia Ausserer 1871:204; Raven 1985:118, 2000:570, 571; Smith 1986:115;

Phlogius Simon 1887:195; Raven 2000. Replaced into synonymy.

Chilocosmia Schmidt & von Wirth 1992:9. First synonymized by Raven 2000.

Selenopelma Schmidt & Krause 1995:22. First synonymized by Raven 2000.

Type species.—*Mygale javanensis* Walckenaer 1837, by original designation.

Diagnosis.—Stridulating organ closely resembles *Chilobrachys* but spines on the outer side of the chelicerae are long (Fig. 6F); the organ tends to be partly obscured by the oral fringe and is certainly indistinct. On the maxillae, the cluster of short shafted bacilli is large and oval and is clustered several rows deep (Fig. 6G). No fringe of hairs overhanging the bacilli. On inner cheliceral face there are three rows of short triangular spines above oral fringe. Leg I shorter and thicker than leg IV, (Raven 1985; Smith 1986).

Description.—Small to middle-sized spiders. Eye tubercle low, clypeus short, ALE > AME. Fovea procurved. Outer cheliceral face with small area of setae, inner face with a few little spines or without; inner margin with row of strong teeth and none on outer margin. Distal labium with cuspules. Sternum red-brown with 3 pairs of sigilla, posterior pair larger. Maxillae with bacilliform setae arranged like combs prolaterally. Palpal bulb nearly spherical, embolus long and curved. Two separated spermathecae, divided or not.

Distribution.—Southeast Asia, South Asia, and Australia.

Remarks.—*Selenocosmia* was erected by Ausserer 1871 from Java and currently has 40 species (subspecies) (Platnick 2008). This genus occurs in a very wide area, from Pakistan and India to New Guinea and Australia. The species has large differences in the shape of stridulating organ and palpal bulb. An exceptional leg formula, 1423, is recorded for *Selenocosmia jiafu* sp. nov. There are also many species variations in this genus.

Schmidt (1995) resuscitated *Phlogius*, but Raven (2000) rejected this interpretation. As Raven (2005) has stated, *S. javanensis*, the type species of the genus *Selenocosmia*, has intercheliceral peg spines. However, all authors admit the absence of a holotype of *S. javanensis* and base descriptions on a presumed type species. Among the three species of

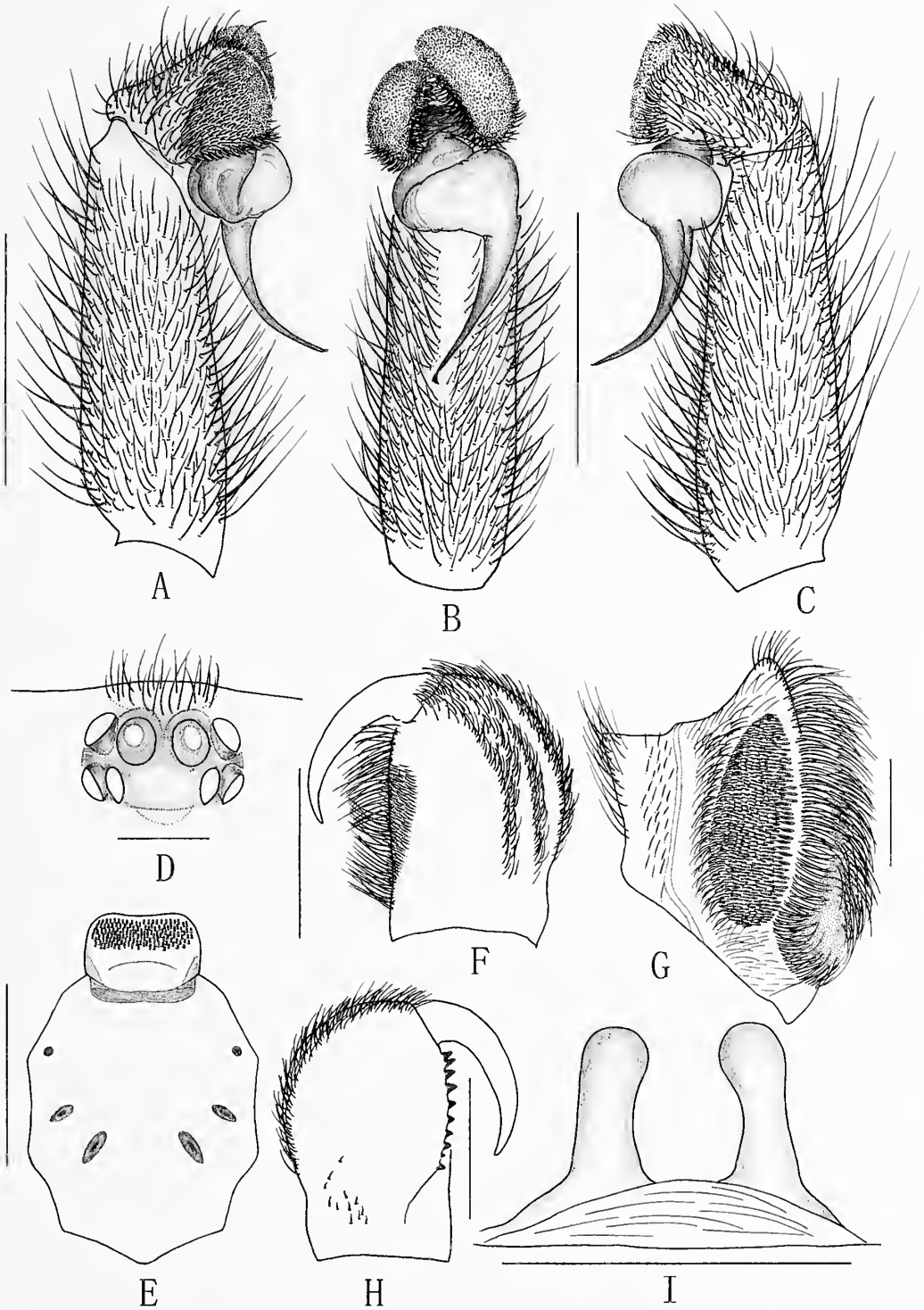

Figure 6.—*Selenocosmia jiafu* sp. nov. A–H. holotype male (MHBU-Ar.T0032). A. Left pedipalp, prolateral view; B. Same, ventral view; C. Same, retrolateral view; D. Eyes, dorsal view; E. Labium and sternum, ventral view; F. Left chelicerae, retrolateral view; G. Maxillae, prolateral view; H. Left chelicerae, prolateral view; I. Paratype female (MHBU-Ar.T0033): spermathecae, dorsal view. Scale bars: 0.5 mm (I), 1 mm (D, G), 3 mm (A–C, E, F, H).

Selenocosmia described in this paper, *S. jiafu* and *S. xinping* both have peg setae between the chelicerae, but *S. xinhuaensis* is without such peg setae. Because we have been unable to find or borrow the type material of *Phlogius* and *Selenocosmia*, we are reluctant to enter a wider taxonomic discussion at this time. Possibly with the assistance of molecular biology and cladistics we may elucidate these problems of classification. We here agree with the suggestion of Raven (2000, 2005) that *Phlogius* is a junior synonym of *Selenocosmia*.

The genus *Selenocosmia* is newly recorded in China, with three new species (*S. jiafu* sp. nov.; *S. xinhuaensis* sp. nov., and *S. xinping* sp. nov.).

KEY TO CHINESE SPECIES OF *SELENOCOSMIA*

1. Female (*S. xinhuaensis* sp. nov. unknown) 2
– Male 3
2. Small area of stridulating organ on prolateral maxillae (Fig. 8G), a pair of thin spermatheca, divided widely (Fig. 8I) ..... *S. xinping* sp. nov.
– Large area of stridulating organ on prolateral maxillae (Fig. 6G), a pair of wide spermatheca, divided narrowly (Fig. 6I) ..... *S. jiafu* sp. nov.
3. Maxillae with row of 5 setae growing in length arranged like a comb prolaterally (Fig. 7G), palpal bulb elliptic, embolus curved at base and without vertical ridge (Fig. 7A, B, C) ..... *S. xinhuaensis* sp. nov.
– Maxillae with a group of lyra setae prolaterally, palpal bulb nearly round, curved embolus with vertical ridge 4
4. Few lyra setae in maxillae occupying a small area, setae similar in size (Fig. 8G), embolus short with wide ridge (Fig. 8C) ..... *S. xinping* sp. nov.
– Many lyra setae in maxillae occupying a large area, lowest setae biggest (Fig. 6G), embolus long with narrow ridge (Fig. 6C) ..... *S. jiafu* sp. nov.

Selenocosmia jiafu sp. nov.
Figs. 6, 19

Selenocosmia huwena: Wang et al. 1993:72, figs. 5, 6 (only paratype male in MHBU, examined).

Type material.—Holotype ♂, MHBU-Ar.T0032, CHINA: Yunnan Province, Menghai County, 21°57′N, 100°29′E, 15 Mar. 1982, J.F. Wang leg. (MHBU); paratype, 1 ♀, MHBU-Ar.T0033, Yunnan Province, Menghai County, 21°57′N, 100°29′E, 2 Aug. 2000, M.S. Zhu leg. (MHBU).

Etymology.—The specific name is a patronym in honor of Professor Jiafu Wang.

Diagnosis.—The new species resembles *S. arndsti* (Schmidt & von Wirth 1991) in having lyra setae in chelicerae and maxillae, but differs in the shape of the palpal organ (Fig. 6A–C). Two separate spermathecae of the new species resembles *S. stirlingi* Hogg 1901 (Schmidt 1995), but the new species is slender in the middle and swollen distally (Fig. 6I), whereas the distal part nearly oval in the latter (Schmidt 1995).

Description.—*Male (holotype):* Total length (including chelicerae) 23.50, cephalothorax 9.71 long, 8.45 wide; abdomen 11.82 long, 7.39 wide. Carapace yellow-brown with reticulated patch and long hairs. Eye group 1.10 long, 1.82 wide (Fig. 6D). Anterior eye row almost straight and posterior eye row slightly recurved. MOA 0.90 long, front width 1.00, back width 1.28. Eye sizes and interdistances: ALE 0.41, AME 0.41, PLE 0.39, PME 0.21; ALE–AME 0.10, AME–AME 0.18, PLE–PME 0.08, PME–PME 0.82. Clypeus 0.31 wide. Fovea transverse, procurved. Chelicerae yellow-brown, with row of 10 promarginal teeth, outer cheliceral face with rows of small setae (Fig. 6F). Labium wider than long, with ca 354 cuspules. Maxillae with a large group of lyra setae prolaterally, the lowest are the biggest (Fig. 6G); with ca 231 cuspules ventrally. Sternum yellow-brown with 3 pairs of sigilla. Palpal tibia swollen. Palpal bulb nearly spherical, embolus long, thin, curved like horn, with vertical ridge (Fig. 6A–C), palpal bulb and embolus 2.80 long. Legs with long and short hairs. Tarsi I–III scopulae full, divided by one or two rows of thin longer bristles, metatarsi I–III with sparse scopulae at base, divided; metatarsus and tarsus IV scopulae divided by rows of bristles, scopula of metatarsus IV very sparse and reaches to half. Metatarsus I and II without ventral middle spine distally, metatarsus III with 5 spines distally arranged like comb, and metatarsus III, IV with 1 dorsal spine. Without spines in others. Femur III short, swollen. Tarsi I–III with 2 claws without denticles, tarsus IV with 3 claws; paired claws with tiny denticles. Palp and legs measurements: Palp 17.32 (6.23 + 3.70 + 5.28 + 2.11), I 31.58 (8.66 + 4.86 + 7.50 + 6.02 + 4.54), II 27.02 (7.71 + 4.22 + 5.91 + 5.17 + 4.01), III 24.28 (6.33 + 3.48+4.33 + 5.28 + 4.86), IV 29.78 (7.92 + 3.38 + 6.76 + 7.50 + 4.22). Leg formula: 1423. Abdomen oval, gray and hairy. PMS 1.39 long, 0.54 wide; PLS 5.53 (1.93 + 1.50 + 1.98), PMS–PMS 0.80.

Female: Total length (including chelicerae) 24.22, cephalothorax 6.68 long, 5.49 wide; abdomen 13.97 long, 7.71 wide. Carapace similar to male. Eye group 0.72 long, 1.33 wide. MOA 0.69 long, front width 0.72, back width 0.90. Eye sizes and interdistances: ALE 0.36, AME 0.31, PLE 0.28, PME 0.18; ALE–AME 0.08, AME–AME 0.10, PLE–PME 0.05, PME–PME 0.59. Clypeus 0.18 wide. Chelicerae with row of 12 promarginal teeth. Labium wider than long, with ca 302 cuspules. Maxillae with ca 156 cuspules ventrally. Tarsus with scopula. Palp and leg measurements: Palp 10.78 (3.70 + 2.22 + 2.43 + 2.43), I 19.05 (5.28 + 3.17 + 4.43 + 3.00 + 3.17), II 14.78 (4.22 + 2.64 + 2.64 + 2.64 + 2.64), III 14.89 (4.33 + 2.64 + 2.64 + 2.64 + 2.64), IV 18.63 (5.28 + 2.75 + 3.80 + 3.80 + 3.00). Leg formula: 1423. Abdomen oval, gray, hairy. Two separate spermathecae, swollen at basal and distal part, divided narrowly (Fig. 6I). PMS 1.34 long, 0.64 wide; PLS 5.12 (2.41+2.14+2.57), PMS–PMS 0.64.

Distribution.—China (Yunnan).

Remark.—The holotype male specimen of this new species is the allotype (paratype) of *Selenocosmia huwena* by Wang, Peng & Xie (1993). Yin & Bao (1995) pointed out that the "allotype male" was a different species and redescribed the male of *S. huwena*. Here, examination of this allotype male demonstrates that it belongs to a new species of the genus *Selenocosmia*.

Selenocosmia xinhuaensis sp. nov.
Figs. 7, 19

Type material.—Holotype ♂, MHBU-Ar.T0034, CHINA: Yunnan Province, Tengchong County, 25°01′N,98°03′E, Xinhua village, 20 Jan. 2005, X.Z. Chen leg. (MHBU).

Etymology.—The specific name refers to the type locality.

Diagnosis.—The new species resembles *S. peerboomi* (Schmidt 1999), but differs by the presence of 5 setae arranged in one row in maxillary lyra (Fig. 7G). *S. peerboomi* has more

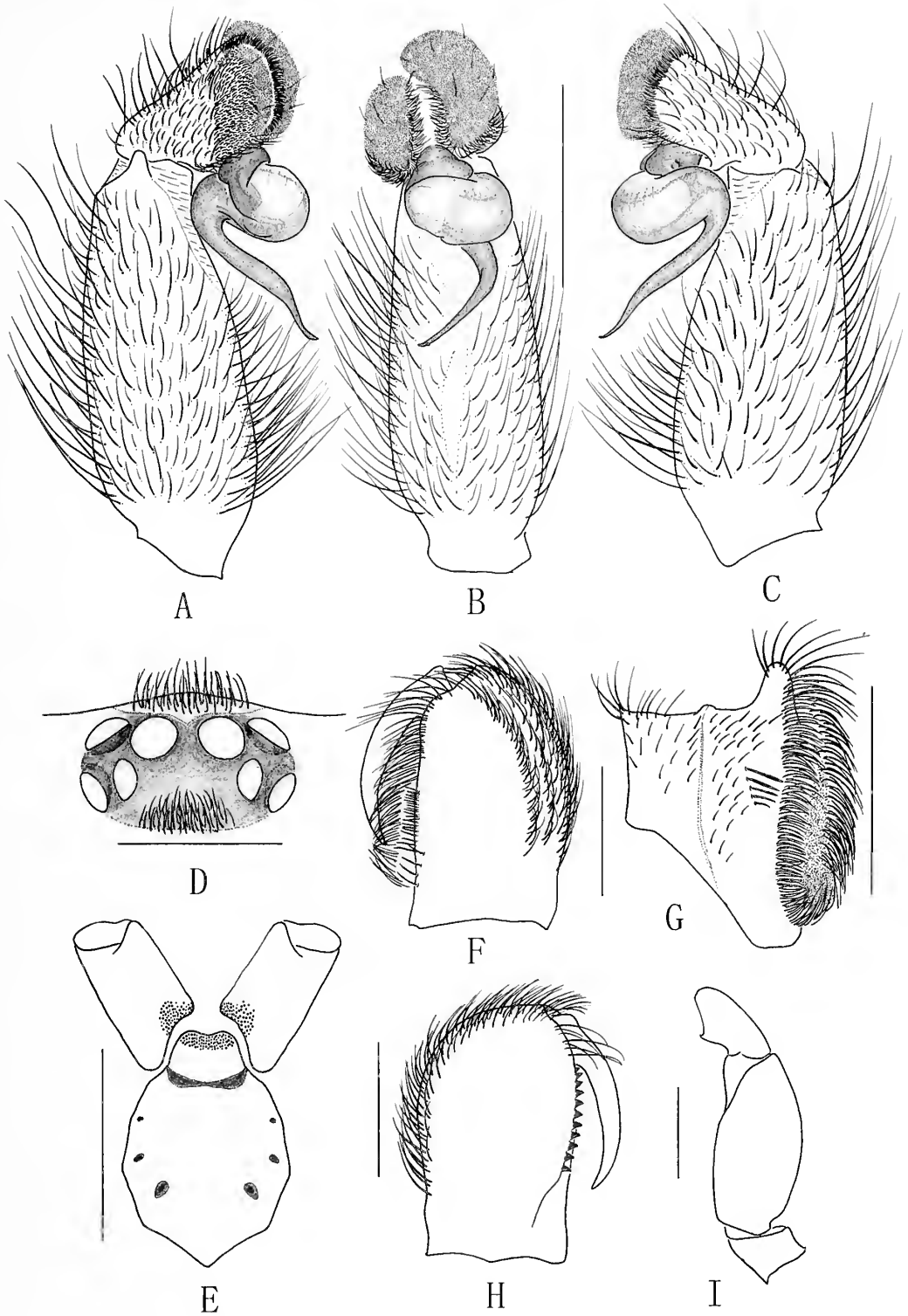

Figure 7.—*Selenocosmia xinhuaensis* sp. nov. A–I. Holotype male (MHBU-Ar.T0034). A. Left pedipalp, prolateral view; B. Same, ventral view; C. Same, retrolateral view; D. Eyes, dorsal view; E. Labium and sternum, ventral view; F. Left chelicerae, retrolateral view; G. Maxillae, prolateral view; H. Left chelicerae, prolateral view; I. Left femur III, retrolateral view. Scale bars: 1 mm (D, G), 2 mm (A–C, E, F, H, I).

than ten setae and many small setae. The shape of the palpal bulb can also distinguish this new species by having an oval palpal bulb and embolus thin, long, curved at base (Fig. 7A–C).

Male (holotype): Total length (including chelicerae) 20.48, cephalothorax 7.39 long, 6.12 wide; abdomen 9.50 long, 5.28 wide. Carapace yellow-brown, with long hairs. Eye group 0.67 long, 1.33 wide (Fig. 7D). Anterior eye row almost straight and posterior eye row recurved. MOA 0.65 long, front width 0.69, back width 1.16. Eye sizes and interdistances: ALE 0.36, AME 0.28, PLE 0.31, PME 0.26; ALE–AME 0.03, AME–AME 0.13, PLE–PME 0.08, PME–PME 0.64. Clypeus 0.15

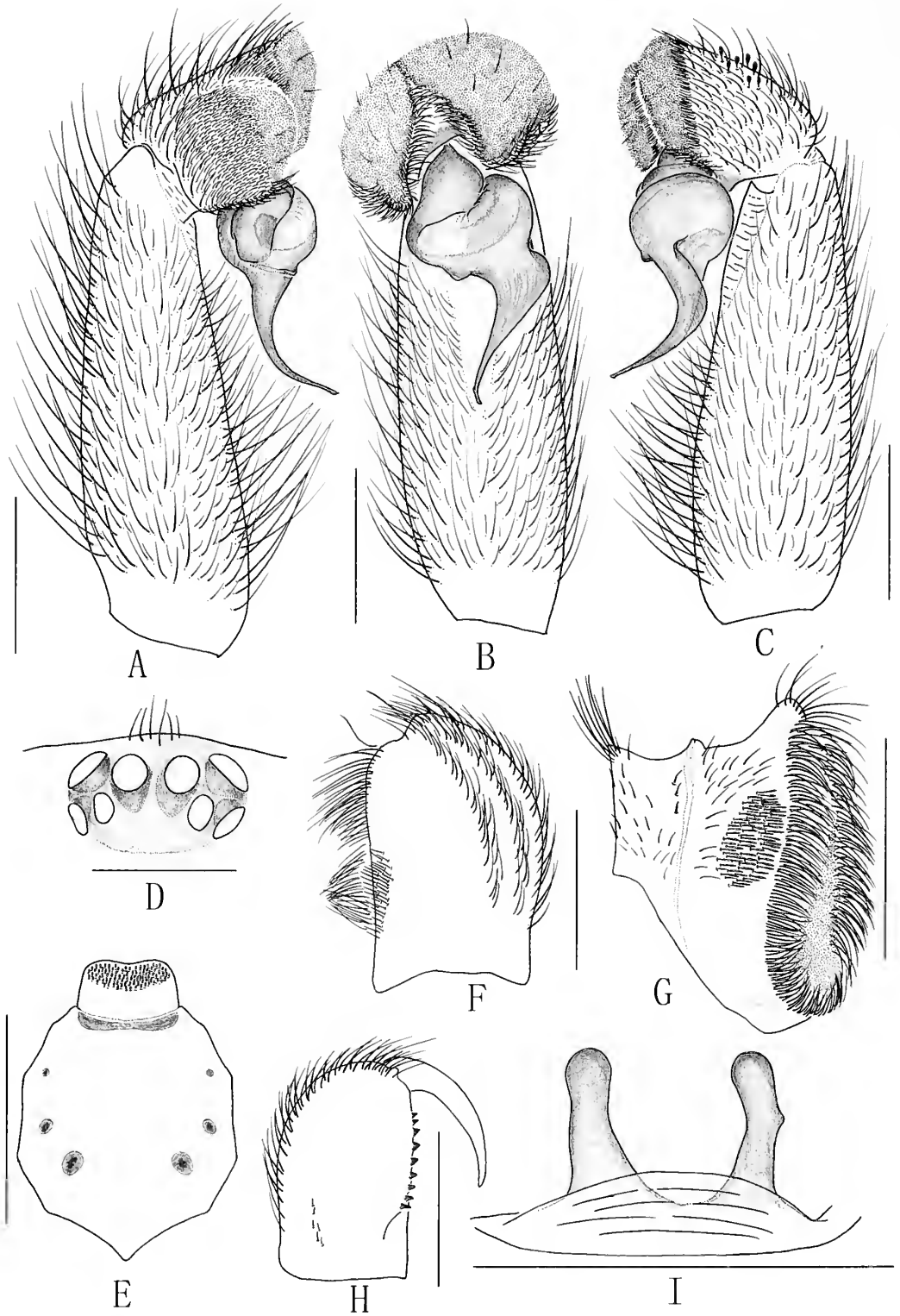

Figure 8.—*Selenocosmia xinping* sp. nov. A–H. holotype male (MHBU-Ar.T0035). A. Left pedipalp, prolateral view; B. Same, ventral view; C. Same, retrolateral view; D. Eyes, dorsal view; E. Labium and sternum, ventral view; F. Left chelicerae, retrolateral view; G. Maxillae, prolateral view; H. Left chelicerae, prolateral view; I. Paratype female (MHBU-Ar.T0037), spermathecae, dorsal view. Scale bars: 0.5 mm (I), 1 mm (A–D, G), 2 mm (E, F, H).

wide. Fovea transverse, procurved. Chelicerae red-brown, 3.59 long, with row of 11 promarginal teeth, outer cheliceral face with many yellow-brown long hairs, lower surface with 4–5 long setae and row of small setae. Labium wider than long, with ca 200 cuspules (Fig. 7E). Maxillae with row of 5 setae growing in length arranged like comb prolaterally (Fig. 7G); with ca 138 cuspules ventrally. Sternum yellow-brown with 3 pairs of sigilla (Fig. 7E). Palpal tibia swollen, with many hairs

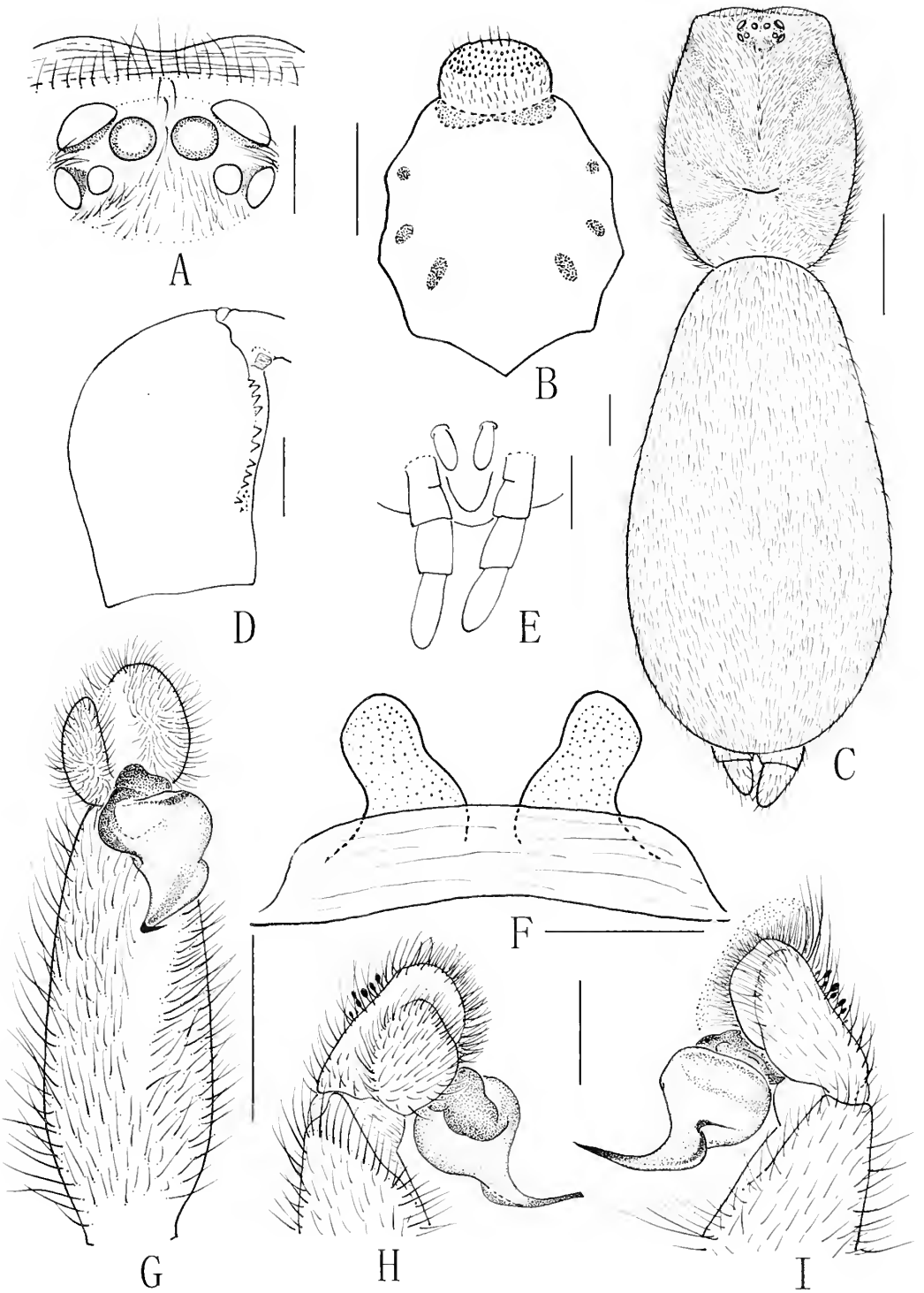

Figure 9.—*Yamia watasei* Kishida, 1920. A–F. female (THU-Ar-0015). A. Eyes, dorsal view; B. Labium and sternum, ventral view; C. Body, dorsal view; D. Left chelicerae, prolateral view; E. Spinnerets; F. Spermathecae, dorsal view; G, H. Male (THU-Ar-0012). G. Right pedipalp, ventral view; H. Same, prolateral view; I. Same, retrolateral view. Scale bars: 0.5 mm (A, F), 1 mm (D, G–I), 2 mm (B, C, E).

outer side, swollen at base. Palpal bulb oval, embolus thin, long, curved at base, with tiny distal groove (Fig. 7A–C). Tarsi I–III scopulae full, divided by one or two rows of thin longer bristles, metatarsi I–III with sparse scopulae at base, divided; metatarsus and tarsus IV scopulae divided by rows of bristles, scopula of metatarsus IV very sparse and reaches to half. Metatarsus II with 3 ventral spines distally, metatarsus III with 5 and metatarsus IV with 3–4, without spines on others. Femur III swollen. Tarsi I – III with 2 claws without denticles, tarsus IV with 3 claws, no denticles on paired claws. Palp and legs measurements: Palp 12.14 (4.43 + 2.64 + 3.59 + 1.48), I 20.91 (6.12 + 3.70 + 4.75 + 3.17 + 3.17), II 18.38 (5.28 + 3.27 + 3.70 + 3.17 + 2.96), III 14.57 (4.01 + 2.64 + 2.64 + 2.64 + 2.64), IV 21.32 (5.70 + 3.17 + 4.22 + 4.75 + 3.48). Leg formula: 4123.

Figure 10.—*Haplopelma hainanum* (Liang et al., 1999), female habitus, from Tongza City, Hainan Province.

Figure 11.—*Haplopelma hainanum* (Liang et al., 1999), habitat, burrow opening, from Tongza City, Hainan Province.

Abdomen oval, gray and hairy. PMS 0.97 long, 0.38 wide; PLS 17.46 long (1.57 + 1.04 + 1.32), PMS–PMS 0.56.

Female: Unknown.

Distribution.—China (Yunnan).

Selenocosmia xinping sp. nov.
Figs. 8, 19

Type material.—Holotype ♂, MHBU-Ar.T0035, CHINA: Hongkong, 22°16′N, 114°09′E, 24 Aug. 1997, X.P. Wang leg.; paratypes, 2♀♀, MHBU-Ar.T0036–0037, Hongkong, 22°16′N, 114°09′E, 24 Aug. 1997, X.P. Wang leg. (MHBU).

Etymology.—The specific name is a patronym in honor of Dr. Xinping Wang, who collected the specimens.

Diagnosis.—The male palpal organ resembles that of *S. arndsti* (Schmidt & von Wirth 1991), but differs in the lyra setae on maxillae. The new species with small group of similar lyra setae in maxillae (Fig. 8G), thinner and longer embolus (Fig. 8A); female with long spermathecae (Fig. 8I), whereas the lyra setae in *S. arndsti* with row of bigger setae, shorter and thicker embolus; female with small and short spermathecae.

Male (holotype): Total length (including chelicerae) 15.40, cephalothorax 6.96 long, 5.89 wide; abdomen 7.60 long, 4.96

Figure 12.—*Haplopelma hainanum* (Liang et al., 1999), habitat, burrow and opening lined with silk (right), small cave with spider barely visible (left), from Tongza City, Hainan Province.

wide. Carapace red-brown with reticulation patch and long hairs on it. Eye group 0.64 long, 1.26 wide (Fig. 8D). Anterior eye row almost straight and posterior eye row slightly recurved. MOA 0.51 long, front width 0.62, back width 0.85. Eye sizes and interdistances: ALE 0.36, AME 0.21, PLE 0.26, PME 0.18; ALE–AME 0.10, AME–AME 0.13, PLE–PME 0.08, PME–PME 0.51. Clypeus 0.15 wide. Fovea

Figure 13.—*Haplopelma schmidti* von Wirth, 1991, female with egg sac, from Pingxiang City, Guangxi Province.

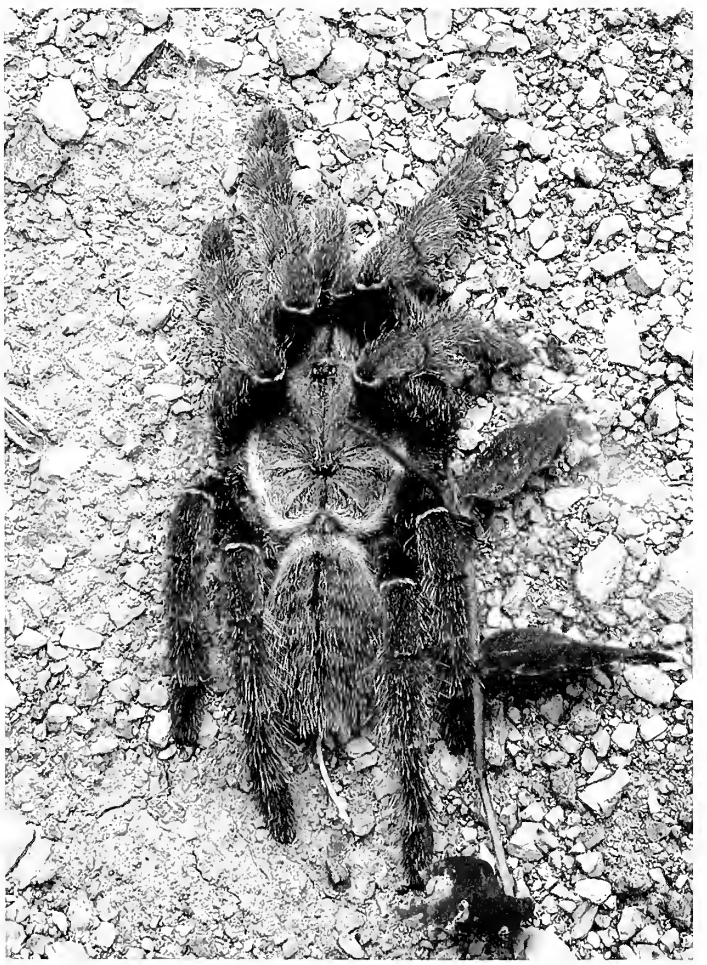

Figure 14.—*Haplopelma schmidti* von Wirth, 1991, female habitus, from Guangxi Province, Pingxiang City.

Figure 15.—*Haplopelma schmidti* von Wirth, 1991, south facing hillside with spider habitat on steep slope, from Guangxi Province, Pingxiang City.

transverse, procurved. Chelicerae red-brown, with row of 8 (9) promarginal teeth, outer cheliceral face with rows of small setae (Fig. 8F). Labium wider than long, with ca 309 cuspules. Maxillae with a small group of lyra setae prolaterally, similar in size (Fig. 8G); with ca 141 cuspules ventrally. Sternum yellow-brown with 3 pairs of sigilla. Palpal tibia with many hairs outer side, swollen at base. Palpal bulb nearly globose, embolus curved like horn, with vertical ridge (Fig. 8A–C), palpal bulb and embolus 1.34 long. Legs with long and short hairs. Tarsi I, II, III scopulae full, divided by rows of thinner longer bristles, metatarsi I, II, III with scopulae sparse at base, divided; metatarsus and tarsus IV scopulae divided by rows of bristles, scopula of metatarsus IV very sparse and reaching to half. metatarsus I with 1 ventral middle spine distally, metatarsus II and III with 3 small spines and metatarsus IV with 4 spines prolaterally. Without spines on others. Femur III short, swollen. Tarsi I–III with 2 claws without denticles, tarsus IV with 3 claws, no denticles on paired claws. Palp and legs measurements: palp 10.34 (3.59 + 2.36 + 3.05 + 1.34), I 19.12 (5.46 + 3.32 + 4.34 + 3.32 + 2.68), II 15.97 (4.55 + 2.84 + 2.95 + 2.95 + 2.68), III 14.52 (4.02 + 2.41 + 2.36 + 3.21 + 2.52), IV 20.73 (5.52 + 2.68 + 4.39 + 5.09 + 3.05). Leg formula: 4123.

Figure 16.—*Haplopelma schmidti* von Wirth, 1991, burrow opening with surrounding silk threads, from Guangxi Province, Pingxiang City.

Abdomen oval, gray, hairy. PMS 1.04 long, 0.35 wide; PLS 3.31 (1.22 + 0.87 + 1.22), PMS–PMS 0.49.

Female: Total length (including chelicerae) 18.00, cephalothorax 8.03 long, 6.75 wide; abdomen 8.45 long, 4.75 wide. Carapace similar to male. Eye group 0.77 long, 1.36 wide. MOA 0.56 long, front width 0.67, back width 0.87. Eye sizes and interdistances: ALE 0.39, AME 0.23, PLE 0.33, PME 0.23; ALE–AME 0.13, AME–AME 0.18, PLE–PME 0.08, PME–PME 0.54. Clypeus 0.26 wide. Chelicerae with row of 9 (10) promarginal teeth. Labium with ca 283 cuspules. Maxillae with ca 117 cuspules ventrally. Palp and legs measurements: palp 12.22 (4.29 + 2.79 + 2.46 + 2.68), I 18.33 (5.36 + 3.755 + 3.75 + 2.68 + 2.79), II 15.91 (5.09 + 2.95 + 2.95 + 2.46 + 2.46), III 14.20 (4.02 + 2.68 + 2.14 + 2.95 + 2.41), IV 20.84 (5.73 + 3.21 + 4.02 + 4.77 + 3.11). Leg formula: 4123. Abdomen oval, gray, hairy. Two separate spermathecae, swollen distally, divided widely (Fig. 8I). PMS 1.08 long, 0.35 wide; PLS 4.73 (1.74 + 1.25 + 1.74), PMS–PMS 0.21.

Distribution.—China (Hong Kong).

Yamia Kishida 1920

Yamia Kishida 1920:303–305; Raven1985:160; Haupt & Schmidt 2004:200; Smith 1986: 140; Zhu & Tso 2005:13.
Baccallbrapo Barrion & Litsinger 1995:21.

Type species.—*Yamia watasei* Kishida 1920, by original designation.

Diagnosis.—Small theraphosid spider lacking stridulation bristles. Cuspules present on labium and ventral side of maxillae. The eye tubercle near anterior margin of the carapace (Fig. 9A), clypeus narrow or absent. Anterior eyes in almost straight row or slightly procurved. Palpal organ bulbous medially, and distinct keel running from bulb along

Figure 17.—*Chilobrachys guangxiensis* (Yin & Tan , 2000), female habitus, from Nan-dao Farm, Hainan Province.

embolus (Fig. 9I). Tibial spur absent. Third claw present on tarsus IV (Haupt & Schmidt 2004; Zhu & Tso 2005).

Description.—See also the description of *Yamia watasei* Kishida 1920.

Distribution.—China (Taiwan).

Remarks.—According to Platnick 2008, genus *Yamia* Kishida 1920 currently contains three species, only one has been reported in China. Since 1990, *Yamia* as *nomen dubium* or *nomem nudum* (Raven 1985; Huber et al. 1996; Song et al. 1999; Platnick 2003). Recently, Haupt & Schmidt (2004) resurrected, discussed *Yamia*, and redescribed the neotype; they also considered that *Baccallbrapo* Barrion & Litsinger 1995 is a junior synonym of *Yamia*, contra Raven (2000) who also considered *Baccallbrapo* Barrion & Litsinger 1995 a junior synonym of *Phlogiellus* Pocock 1897.

Raven (2005) suggested that if the lyra had been secondarily lost in *Yamia watasei* Kishida then it may be better placed in *Phlogiellus*. But he did not resolve the relationship of *Yamia* and *Phlogiellus*. *Yamia* lacks stridulation setae, has ALE larger than PLE, and the fovea is slightly procurved. *Phlogiellns* has stridulation setae, ALE are similar to PLE, and the fovea is strong procurved. We consider each to be a valid genus, and therefore reject the suggestion of Raven (Raven 2000) who proposed *Yamia* to be a junior synonym of *Phlogiellus*.

The description of genus *Yamia* is in accordance with *Baccallbrapo* in eye size, eye arrangement, palpal organ, leg scopulae and the number of tarsal claws (Haupt & Schmidt 2004; Barrion & Litsinger 1995). Also the distribution of *Yamia* (from Lanyu Island, Taiwan) and *Baccallbrapo* (from the northern Philippines) is reasonably close. We agree with the suggestion of Haupt & Schmidt (2004) who believe *Baccallbrapo* to be a junior synonym of *Yamia*.

Yamia watasei Kishida 1920
Figs. 9, 19

Yamia watasei Kishida 1920:299, figs. 1, 2 (holotype female, lost); Kayashima 1943:38; Li 1964:14, fig. 2c; Song et al. 1999:41; Schmidt 2003:244; Haupt & Schmidt 2004:199, figs. 1–7 (male, neotype in ZSM, not examined); Zhu & Tso 2005:13, figs. A–I.

Materials examined.—3♂♂, 1♀ (THU-Ar-01-0011, 0012, 0013, 0015), Taiwan: Taidong County, Lanyu Islang, 22°45′N, 121°08′E, 2 Mar. 2001, D.Q. Ye leg.

Diagnosis.—*Yamia watasei* differs from its relative, *Baccallbrapo bundokalbo* Barrion & Litsinger 1995, in that the male has a longitudinal keel running from the bulb along embolus and has a short embolus (Fig. 9H). Scopulae of metatarsi and

Figure 18.—*Chilobrachys guangxiensis* (Yin & Tan , 2000), burrow and opening lined with silk, from Nan-dao Farm, Hainan Province.

tarsi I–III undivided; scopulae of metatarsi and tarsi IV divided by rows of setae in male. Scopulae of female all divided by setae. Spermathecae one pair and bulbous (Fig. 9F), with its base thickened. Without ovate setae on dorsum of tarsi.

Redescription.—*Female:* Iotal length (including chelicerae) 18.81: cephalothorax 6.57 long, 4.95 wide; abdomen 9.63 long, 5.49 wide. Eye group 0.58 long, 1.05 wide (Fig. 9A). Eye interdistances: AME : ALE : PME : PLE (0.25 : 0.33 : 0.13 : 0.23). Clypeus 0.15 wide. Chelicerae and prolateral maxillae lacking stridulating bristles. Labium wider than long, with ca 316 cuspules (Fig. 9B). Maxillae with ca 126 cuspules ventrally. Sternum with 3 pairs of sigillae. Scopulae of metatarsus IV sparse, occupying 1/2 of its total length, divided by setae. Tarsi I–IV with 2 claws, tarsus IV with third claw, 0–2 denticles on paired claws; dorsally with 2 rows of club-shaped setae. Spermathecae one pair and bulbous, with its base thickened (Fig. 9F).

Male: Total length (including chelicerae) 14.20–14.22. Total length 14.22; cephalothorax 5.67 long, 6.30 wide; abdomen 6.03 long, 3.15 wide. Labium with ca 268 cuspules. Maxillae with ca 88 cuspules ventrally. Scopulae of metatarsi and tarsi I–II full, undivided. Scopulae of legs III and IV like female. Leg I lacking tibial spur. Palpal bulb almost globular, with longitudinal keel running from bulb along embolus (Fig. 9G–I).

Distribution.—China (Taiwan).

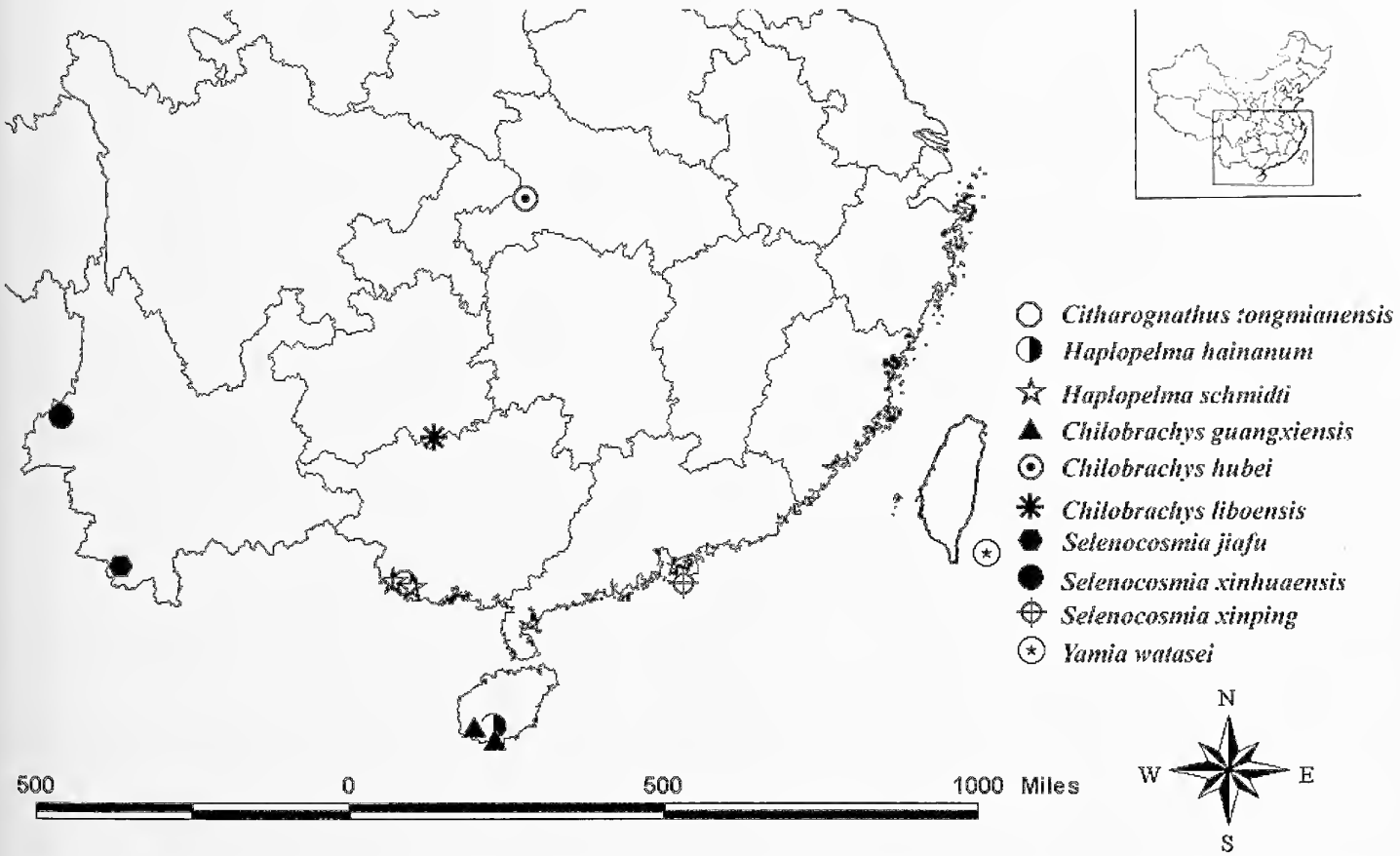

Figure 19.—Records of 10 species of Theraphosidae from China. 1. *Citharognathus tongmianensis*; 2. *Haplopelma hainanum*; 3. *Haplopelma schmidti*; 4. *Chilobrachys guangxiensis*; 5. *Chilobrachys hubei*; 6. *Chilobrachys liboensis* sp. nov.; 7. *Selenocosmia jiafu* sp. nov.; 8. *Selenocosmia xinhuaensis* sp. nov.; 9. *Selenocosmia xinping* sp. nov.; 10. *Yamia watasei.*

Natural history.—*Yamia watasei* is locally rather abundant, apparently living in shadowy forests which are close to the natural condition. It prefers to build the entrance to its subterranean system of silk tubes under stones, apparently in order to avoid direct access of rain water. The soil must be moist. Prey consists mostly of insects seeking shelter under stones. After catching such prey, which touched the silken mouth of a tube's entrance, the spider returns back into the tube system (Haupt & Schmidt 2004).

DISCUSSION

The Theraphosidae spiders of China are poorly known and up to now only five genera and ten species have been reported from China. The members of this family occupy only about 1% of the world's known species. Recorded localities are limited to Hainan, Guangxi, Guizhou, Yunnan, Hongkong, and Taiwan of China, all tropical. (Fig. 19). The arachnologists of China should devote more time and effort to this family. Special attention should be paid to the search for unknown males and females with the goal of learning more of the biogeography and phylogeny through the study of their morphology. More investigation on this family will provide new perspectives for further research.

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Non-random patterns of spider species composition in an Atlantic rainforest

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Abstract. Spider species respond differently to variations in habitat structure; thus, differences in habitat structure may be responsible for variations in species composition of assemblages. However, little information exists on patterns of variation in spider species composition in tropical rainforests. We collected spiders and measured five different microhabitat characteristics in 20 sampling plots distributed among secondary and primary forest patches in an Atlantic rainforest, Brazil. Using multivariate analysis (non-metric multidimensional scaling - NMS), we checked for the existence of non-random patterns in the species composition of aerial (AG) and ground (GG) macroguilds, respectively. We also explored the relationships of those patterns with gradients in microhabitat characteristics and the influence of forest type (primary or secondary forest). We detected non-random patterns in spider species composition unrelated to microhabitat characteristics but differing between primary and secondary forest plots for both macroguilds. We discuss possible implications for studies of spider species composition and spider conservation in tropical forests.

Keywords: Araneae, community ecology, microhabitat gradients, guilds, conservation, tropical forests

Resumo. As espécies de aranhas respondem de modo distinto a variações na estrutura do habitat. Por esta razão, diferenças nestas estruturas poderiam ser responsáveis pela variação na composição de espécies das assembléias. Contudo, existe pouca informação a respeito de padrões na variação da composição das assembléias de aranhas em floresta tropical. Neste trabalho, foram coletadas aranhas e mensuradas cinco diferentes características de micro-hábitat em 20 unidades amostrais distribuídas em áreas de floresta primária e secundária de floresta tropical Atlântica. Utilizando análises multivariadas (ordenação multidimensional não métrica – NMS), procurou-se a existência de padrões não aleatórios na composição de espécies de aranhas de macroguildas aéreas (AG) e de chão (GG), respectivamente. Investigou-se também, a relação destes padrões com gradientes nas características de micro-hábitat e a influência do tipo de floresta (floresta primária e secundária). Foram detectados padrões não aleatórios na composição de espécies de aranhas, não relacionados às características de micro-hábitat, todavia influenciados pelo tipo de floresta. Discute-se, portanto, a possível problemática de estudos que abordam composição e conservação de espécies de aranhas em florestas tropicais.

The knowledge of species composition patterns can be a useful tool for habitat management planning directed towards conservation (Primack & Rodrigues 2001). However, with the disturbance of the last remnants of the original habitat (Myers et al. 2000) we might loose the chance of rescuing the original patterns of local spider species distribution.

Spiders select different structures for living in their habitats (Robinson 1981; Greenstone 1984; Heikkinen & MacMahon 2004) and their populations respond to structural gradients in the habitat (Colebourn 1974; Lubin et al. 1993). Different characteristics of spider assemblages, like abundance of some groups, richness, or diversity, also change along gradients in vegetation density (Rypstra 1983, 1986; Balfour & Rypstra 1998; Gunnarsson 1988, 1990; Halaj et al. 1998). This is a result of the different responses of species exposed to the same gradients (Raizer & Amaral 2001; Wagner et al. 2003). In this way, gradients in vegetation structure might be responsible for gradients in species composition.

Most previous studies of tropical forest spider assemblages have compared richness estimators (Álvares et al. 2004; Sorensen 2004; Candiani et al. 2005; Indicatti et al. 2005; Oliveira-Alves et al. 2005; Dias et al. 2006; Nogueira et al. 2006), diversity and community structure indices between different rainforest fragments (Greenstone 1984; Russel-Smith & Stork 1994; Floren & Deeleman-Reinhold 2005; Barlow et al. 2007). Studies on assemblage composition in rainforest fragments have been limited to sunny regions of rainforests, such as canopies (Russel-Smith & Stork 1995) and clearings (Peres et al. 2007). Therefore, we know almost nothing about the patterns of variation in spider species composition in the shaded regions of rainforests.

Arachnid assemblages in primary forest fragments exhibit higher spatial species turnover when compared to secondary forests (Floreen & Deeleman-Reinhold 2005; Nogueira et al. 2006; Barlow et al. 2007; Bragagnolo et al. 2007). Primary forest fragments have usually been considered homogeneous in their conditions when compared to secondary fragments (Floreen & Deeleman-Reinhold 2005; Nogueira et al. 2006; Barlow et al. 2007; Bragagnolo et al. 2007). However, the best preserved forest remnants consists of a mixture of secondary and primary forest, supporting the possibility of gradients in structural characteristics (as they function as microhabitats for spiders) to which the spatial species turnover might be related.

The exuberant diversity of arthropods in tropical areas requires a considerable effort for collecting, classifying, and analyzing local taxocenoses (Lawton et al. 1997). Höfer & Brescovit (2001) divided Neotropical spiders into guilds the members of which forage in the same microhabitats. Classifications like this allow us to separate the high levels of diversity present in tropical rainforests into ecologically recognizable and analytically treatable groups. Therefore, it becomes easier to associate gradients of species composition to gradients of microhabitat availability.

In this study, we looked for non-random patterns of spider composition in aerial and ground spider guilds in an Atlantic rainforest fragment in northeastern Brazil, and tested if they were related to gradients of microhabitat availability. We also tested if species composition and microhabitat gradients differ between primary and secondary forest fragments. Finally, as spider species inventories are scarce in this region of South America, we provide a list of species with abundance data as online material.

METHODS

Field work took place in the Fazenda Camurujipe (12°30′5″S, 38°2′19″W), a private farm, owned by the Garcia D'Ávila foundation, and located in the in Açu da Torre village, Mata de São João district,

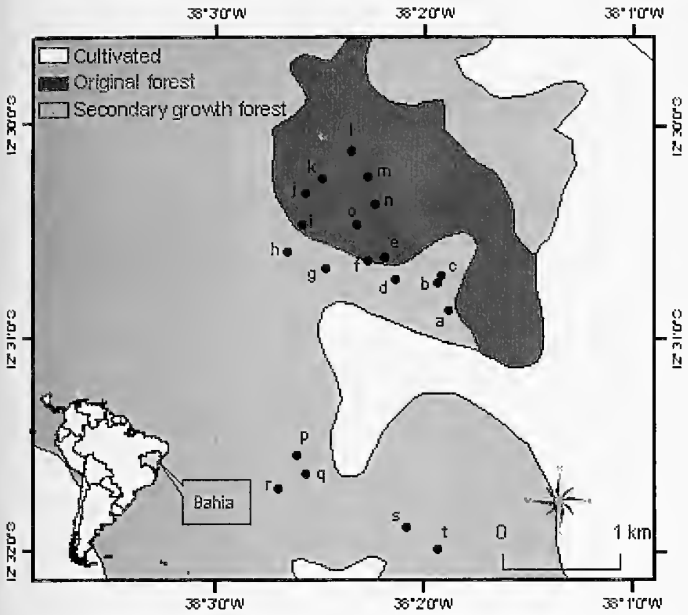

Figure 1.—Map of study area, with position of sampling plots among vegetation types, and location of study site inside the state of Bahia, northeastern Brazil.

100 km north to Salvador de Bahia, northeastern Brazil. This fragment contains 1,390 ha of ombrophylous lowland rainforest and presents a softly undulated geomorphology, typical for the region (Ab'saber 1977). A part of the forest was partially logged 35 years before but primary forest still exists. This fragment is one of the best preserved in the northern littoral of Bahia. This makes it critically important for conservation and study of the arachnofauna since significant forest patches are virtually nonexistent in Northeastern Brazil (Morellato and Haddad 2000). Mean temperatures in this region vary between 21°C and 26°C. Annual rainfall reaches 2000 mm, and rains are more concentrated from March to July (Instituto Nacional de Meteorologia. Online at http://www.inmet.gov.br).

Sampling design.—We sampled in 20 rectangular plots of 30 m × 5 m identified by letters (a, b, c, d...o; Fig. 1). Two complementary sampling methods were used: beating tray and hand collecting by visual searching. We used the beating-tray method to sample 15 bushes (all ≤ 3 m in height) of different species per plot, selected haphazardly. In each plot we invested an effort of two persons per hour in each expedition of active diurnal searches. We sampled each plot once in each of two five-day expeditions (January and March 2006). We distributed the plots systematically in the forest fragment. To do this, we walked 5 minutes along the main trails and then randomly chose the side of the trail and the distance from the plot to the trail (10 to 100 m). After a plot was established, we came back to the main trail and repeated the process. The forest fragment presented two forest types (data from the state's environmental resources council, Superintendência de Políticas Florestais, Conservação e Biodiversidade. Online at http://www.meioambiente.ba.gov.br/); thus we placed 12 plots in secondary forest (35 years old) and 8 in original primary forest (Fig. 1). The taxonomist, A.D. Brescovit, classified the specimens to species or morphospecies level. Specimens were deposited in the Butantan Institute's Collection (IBSP, curator A.D. Brescovit) and the Zoology Museum of the Federal University of Bahia (MZUFBA, curator T.K. Brazil).

Measurement of microhabitat availability.—In each plot we measured the availability of five different microhabitat characteristics. Leaf litter cover and grass cover were estimated according to Fournier's scale (Fournier 1974). We counted the number of fallen trunks with more than 15 cm in circumference and saplings with less than 15 cm in circumference. We also measured the diameter at breast height of all trunks with more than 15 cm in circumference. All measurements were made within a 5 m radius around 4 points placed 10 m apart.

Analysis.—We deleted all singletons from the analysis, since their position in one plot does not give reliable information on their ecological requirements. We divided the species into two "macroguild" matrices, according to Höfer & Brescovit (2001). The first macroguild matrix (aerial macroguild, AG), included species belonging to guilds that forage at medium height in the understory such as nocturnal aerial runners (Anyphaenidae, Clubionidae, Mimetidae, Salticidae, Segestriidae), aerial ambushers Thomisidae), sedentary sheet weavers (Pholcidae and Pisauridae), aerial space web builders (Dictynidae and Theridiidae), aerial orb weavers (Araneidae, Tetragnathidae, Uloboridae, and Theridiosomatidae), nocturnal aerial ambushers (Senoculidae, Sparassidae, and Salticidae), and diurnal aerial hunters (Oxyopidae). The ground macroguild (GG) included species belonging to guilds that forage on the ground: diurnal ground runners (subfamilies Castianeirinae and Corinninae from Corinnidae), nocturnal ground weavers (Deinopidae and Dipluridae), diurnal ground weavers (Mysmenidae and Linyphiidae), ground ambushers (Idiopidae), and leaf litter stalkers (Miturgidae). The morphospecies belonging to Euophryinae (Salticidae), *Nothroctenus* Badcock 1932, *Celaetychaeus* Simon 1897 and *Ctenus* Walckenaer 1805 (Ctenidae) should belong to the aerial macroguild according to the classification proposed by Höfer & Brescovit (2001). However, our observations indicated that they forage on the leaf litter and thus we included them in the ground macroguild. A tree fell over plot "h" between the sampling trips; therefore we decided to remove it from the ordinations but maintained it in the total counts and the species list.

To detect non-random variation axes in species composition, we performed a non-metric multidimensional scaling (NMS) analysis on each macroguild matrix using PC-ORD® (see McCune & Grace (2002) for a comprehensive explanation of NMS method). NMS orders the plots on axes according to their similarity in species composition. In this way, the relative similarity in species composition among plots is represented by the differences between their axis scores. NMS does not assume linear relationships between species and environmental gradients. Because of that it is especially appropriate for reduction of species composition matrices, whieh seldom fulfil those assumptions. Our choices for performing the analysis followed recommendations from McCune & Grace (2002). First, we performed an exploratory analysis in the PC-ORD® program (McCune & Grace 2002) to detect the best options for representation of variation in species composition. We used the following choices: 6 possible dimensions, instability criterion of 0.005, 500 iterations, 999 runs with real data and 999 runs with randomized data. As the exploratory analysis indicated that one axis ordination was recommended, we represented the variation of each macroguild matrix on one axis. Abundances of each species in each plot were divided by the total of spider caught in each plot. Relative abundances were analyzed, the Bray Curtis coefficient was selected as the distance measure, and we used a random starting point and 500 runs with real data to find the best representation of the data on one axis (McCune & Grace 2002). We applied a Monte Carlo test, with 999 runs of randomized data, to test if our ordination was expected from a randomized version of the composition matrix. Our criterion for evaluating stability of the solution was standard deviation in stress equal to or less than 0.002, with 100 iterations to evaluate stability and 500 as the maximum number of iterations. Finally, the correlation of the distances between plots in the original abundance matrices with the distances in new ordered matrices was evaluated using a Mantel's test. We calculated the significance of the correlation via Monte Carlo randomization method with 999 randomizations.

We represented the main gradients in microhabitat descriptors across all the plots by performing a Principal Component Analysis

Table 1.—Descriptive statistics of microhabitats, measured in an Atlantic Rainforest fragment, northeastern Bahia. Abbreviations: DBH, diameter at breast height; GC, grass cover; LC, leaf litter cover; NS, number of saplings; NFT, number of fallen trunks.

	n	Range	Min.	Max.	Mean	S.D.
Grass cover (%)	19	55.0	25.0	80.0	57.1	16.9
Leaf litter cover (%)	19	15.0	85.0	100.0	96.6	5.3
Number of fallen trunks	19	19.8	4.0	23.8	13.1	6.1
Diameter at breast height (cm)	19	457.3	214.5	671.8	439.2	153.3
Number of saplings	19	24.8	7.6	32.4	18.0	5.9

(PCA), based on the correlation matrix and using varimax rotation (SPSS 12 for windows program). We tested the relationship between NMS and PCA axes via linear regression. To test the difference in species composition and microhabitats between primary and secondary forest plots, we first performed a Levene test to detect differences in composition variation (beta diversity), and a Welch *t*-test to detect differences in NMS and PCA scores (differences in species composition and microhabitat availability).

RESULTS

Sampling results.—From a total of 2082 collected spiders, 654 adult specimens were classified into 26 species and 104 morphospecies. The 130 species were distributed in 32 families. The four most abundant families were Salticidae with 32 species (24.2% of individuals), Pisauridae with only one species (13%), Theridiidae with 27 species (12.5%) and Thomisidae with 9 species (9.6%) (see online list at http://www.redezoo.ufba.br/Specieslist.htm). The most abundant and species rich guild was the nocturnal aerial runners with 741 specimens and 46 species. Sedentary sheet weavers was the second most abundant with 359 specimens. The second richest guild was the aerial space web builders with 27 species, followed by aerial orb weavers with 24 species. Two guilds, ground ambushers and leaf litter stalkers, were represented only by singletons, thus they were deleted from the analyses.

Gradients in species composition.—NMS detected a single non-random axis of variation for each of the two macroguilds (AG: 62 species, 15 families, Montecarlo $P = 0.004$, stress: 29.5%, instability: 0.025; GG: 9 species, 4 families, Montecarlo $P = 0.15$, stress 27.2%, instability: 0.015). The Mantel test showed that 66% of the original differences in species composition from AG and 73% from GG were explained by the NMS axes. Stress values close to 30% are high. However, stress depends on the number of species in the matrix (McCune & Grace 2002), which is very high when related to the number of plots (62 species in 20 plots) in the case of AG matrix. The instability criterion was also not met for the AG axis. This means that the ordination may give different results depending on the number of iterations. Due to this fact, we performed the ordination of the AG matrix several times and observed that the ordination of the non-random gradient in species composition was indeed constant, going from the plots a, b, c, d, o, to plots j, k, l, m.

Reduction of microhabitat descriptors.—PCA generated two axes (PCs) that represented a reasonable part of the total variation (74.5%) in microhabitat characteristics. The first axis (PC1: 44% of total variation), represented number of saplings (loading: 0.914), and leaf litter cover (loading: 0.871). The second axis (PC2: 30.5% of total variation) represented increasing diameter breast height of trees (loading: 0.758) and grass cover (loading: 0.689), and decreasing number of fallen trunks (loading: −0.729). A description of environmental variables is presented in Table 1.

The multiple regression analysis showed that none of the two PCs were significantly related to the species composition axes (AG: PC1: b = 12016.14; $P = 0.59$; PC2: b = 4616.160; $P = 0.83$; GG: PC1: b = 9529.61; $P = 0.72$, PC2: b = 7086.47; $P = 0.84$). This indicates that the microhabitat characteristics measured did not affect the species composition gradients detected by the NMS analyses. Visually assessed normality of residuals did not deviate seriously from it.

Comparison of primary and secondary forest.—Despite the fact that the two macroguilds showed more variation in species composition in the primary forest (Mean ± SD (range); AG: 0.31 ± 1.39 (−2.61 to 2.25); GG: 0.83 ± 0.93 (−0.80 to 2.16) than in the secondary forest (AG: −0.13 ± 0.58 (−0.86 to 1.07); GG: −0.65 ± 0.40 (−1.36 to −0.07), the differences were significant only for the AG NMS axis (Levene's test $P = 0.018$). Welch's *t*-test for unequal variances showed that primary and secondary forest types differed in species composition (NMS scores on the axis generated) only with respect to GG ($t = 4.377$, $df = 10$; standard error of difference 0.339; $P = 0.001$). Differences among PCA plot scores were not significant between primary and secondary forest plots (PC1: $t = 0.9236$, $df = 15$, standard error of difference = 0.467; $P = 0.3703$; PC2: $t = 0.4588$, $df = 16$, standard error of difference = 0.453; $P = 0.6525$). Thus, we found no gradients in microhabitat availability between primary and secondary forest plots that might explain the differences in species composition.

DISCUSSION

Both aerial and ground macroguilds showed one non-random axis of variation in species composition. Significant variations in species composition of tropical spider assemblages have been reported from comparisons between different fragments, usually related to different stages of ecological succession (Floren & Deeleman-Reinhold 2005; Nogueira et al. 2006) or when comparing *Eucalyptus* plantations with forest fragments in different stages of regeneration (Barlow et al. 2007). Nogueira et al. (2006) suggested that differences in vegetation structure between fragments in different forest stages of succession might determine the variation in spider species composition, since it is related to microhabitat diversity and microclimate conditions.

The availability of some microhabitats has been widely recognized as important for spider populations (Colebourn 1974; Lubin et. al 1993) and guilds (Rypstra 1983, 1986; Greenstone 1984; Balfour & Rypstra 1988; Gunnarsson 1988, 1990). In our study, however, variation in the availability of different vegetation attributes, such as grass cover, number of saplings, number of dead trunks and diameter at breast height, did not show any effect on spider species composition.

The extremely high spider species richness typical for tropical regions makes it difficult to detect a single variable that influences whole assemblages. However, we grouped the species sampled by similarity in microhabitat use (aerial and ground macroguilds) and then related the macroguilds to the main gradients in microhabitat availability (PC1 and PC2), representing several microhabitat descriptors at the same time. Theoretically, this should increase our ability to find an influence on species composition. As shown in Table 1, the ranges of variation in microhabitat availability were variable among the different descriptors. However, they might not have been enough to influence the relative abundance of an important number of spider species. Russel-Smith & Stork (1995) studied spider species composition along the canopy of a humid tropical forest in Borneo and did not find any influence of tree structural and taxonomic variation on species composition. Peres et al. (2007) found

differences in composition of spider assemblages in an Atlantic forest fragment when comparing natural treefall gaps with the surrounding forest. Additionally, they found significant differences in habitat structure and microclimate conditions. These results suggest that gradients of spider species composition in tropical forests might be related to strong variations in microclimate conditions, such as those related to treefall gaps, instead of variation in the availability of different physical structures or microhabitats. However, additional experimental studies on rainforest spiders' tolerance to perturbation in microhabitat availability should illuminate their sensibility to human made perturbations.

Another reason for not finding significant relationships between microhabitat availability and non-random changes in the composition of spider assemblages are that other, stronger, factors are affecting them. In our study, both axes of species composition were significantly affected by the stage of ecological succession of the patch: AG presented higher variation in species composition among plots from the primary forests, and species composition was significantly different for GG. Since only one patch of each stage of regeneration was available in the fragment, the samples are arguably non-independent because plots in the primary forest are neighbors in one part of the fragment (see Fig. 1). Despite the plots being geographically more dispersed in the secondary forest patch, none of the two macroguilds showed less variation in species composition inside the primary forest (in fact, AG showed significantly higher variation). This is contrary to what would be expected if distance was related to similarity in composition. Tropical forests are generally considered as homogeneous systems when they are compared (Floren & Deeleman-Reinhold 2005; Mathieu et al. 2005; Nogueira et al. 2006; Barlow et al. 2007; Bragagnolo et al. 2007). The significant differences found for both macroguilds and higher species composition variation of AG in primary forest indicate that the history of perturbation inside a tropical forest fragment may be an important generator of spatial variation in species composition. Since tropical forests could present a heterogeneous mix of successional stages, therefore affecting species composition, future authors should be cautious with the selection of sampling sites inside their considered "primary" forests. We found higher variation in species composition in primary forest, but this was only significant for AG. Our results for AG agree with Floren & Deeleman-Reinhold (2005), who found that spatial species turnover was highest in primary forest, compared to isolated forest fragments. This supports the idea that higher spatial turnover in spider species composition is related to better preserved tropical forests and suggests two possibilities: a) that ground spiders might recover the spatial variation in species composition faster; b) that ground spiders might be more tolerant to habitat changes than aerial spiders, maintaining similar levels of spatial variation in species composition in situations of habitat change.

In our study we did not find gradients of microhabitat availability to be influenced by forest type (primary and secondary), nor did we find a relationship between gradients in microhabitat availability and spider species composition. Probably other habitat characteristics than those we measured can better express the subtle variation between forest types inside the same fragment and might be generating the changes in species composition. The largest distance between plots was less than two kilometers and the forest extends continuously between the plots. However, primary and secondary patches exhibited significantly different species composition for GG and a significantly increased variation between plots in secondary forest for AG.

What could be preventing the restitution of composition and composition variability in those macroguilds of spiders after thirty five years of recovery? The low population density of most spider species in our study suggests a possible hypothesis, testable and relevant to conservation. This is that the low population densities of most spider species in tropical forests may make them bad re-colonizers. If low population density deters tropical forest spiders from long term recolonization in adjacent patches of habitat, even with the highest investments and the best techniques in vegetation restoration, most spider species might be doomed to extinction in tropical forests. Density dependence tests in recolonization ability of spider species, controlling for microhabitat dependence, could shed light on this problem.

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Mesabolivar brasiliensis (Moenkhaus 1898) and *Mesabolivar cyaneotaeniatus* (Keyserling 1891) (Araneomorphae, Pholcidae): close relationship reinforced by cytogenetic analyses

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Abstract. Pholcidae is the most diverse family among haplogyne spiders but only 15 species have been analyzed cytogenetically. These studies revealed that the diploid number varies from 2n = 15 to 2n = 32, that there are three types of sex chromosome systems in males (X, X_1X_2 and X_1X_2Y), and that the chromosomes are predominantly biarmed. Within the genus *Mesabolivar*, only *Mesabolivar luteus* (Keyserling 1891) has been karyotyped, and it showed 2n = 15 = 14 + X, with all chromosomes being metacentric. In the present work, we characterize the mitotic and meiotic chromosomes of *Mesabolivar brasiliensis* (Moenkhaus 1898) and *Mesabolivar cyaneotaeniatus* (Keyserling 1891). Male mitotic metaphases of the two species showed the diploid number 2n = 17 = 16 + X; oogonial cells of *M. brasiliensis* showed 2n = 18 = 16 + XX. In both species, the chromosomes were exclusively biarmed, and the X chromosome was the largest element of the karyotype. Diplotene spermatocytes of the two species exhibited 8II + X and the occurrence of only one terminal or interstitial chiasma per bivalent. In *M. cyaneotaeniaus*, metaphases II with n = 9 = 8 + X and n = 8 were found, indicating the regular segregation of all chromosomes during meiosis I. Mitotic metaphases of *M. brasiliensis* stained with CMA_3/DAI DAPI revealed GC-rich chromatin in the terminal region of almost all autosomes, especially in pair 2. An earlier revision of the New World pholcids grouped *M. brasiliensis* and *M. cyaneotaeniatus* in a "southern group" and placed *M. luteus* in a "miscellaneous group." A molecular study showed a closer relationship between *M. brasiliensis* and *M. cyaneotaeniatus* than between *M. luteus* and either of these two species. The 2n = 17 found in *M. brasiliensis* and *M. cyaneotaeniatus* corroborates this hypothesis, given that *M. luteus* has a diploid number of 2n = 15.

Keywords: Chromosome, Haplogynae, meiosis, sex chromosome system, spider

According to Platnick (2008), the family Pholcidae Koch 1851 includes 999 extant species, and thus constitutes the most diverse family among haplogyne spiders. A phylogenetic analysis based on morphological characters separated pholcids into four clades: "ninetines," "pholcines," "holocnemines," and the "New World clade" (Huber 2000). The genus *Mesabolivar* González-Sponga 1998, which ranges from northern South America to northern Argentina, is included in the "New World clade" and possesses 45 species (Huber 2000, 2008). Moreover, the genus is divided into four operational groups based on morphological characters: a "northern group with spines on male metatarsi," a "northern group without spines on male metatarsi," a "southern group," and a "miscellaneous group." The species *Mesabolivar brasiliensis* (Moenkhaus 1898) and *Mesabolivar cyaneotaeniatus* (Keyserling 1891), both part of the "southern group," are distributed in southern and eastern Brazil and northern Argentina (Huber 2000, 2008).

Until now, only 15 pholcid species have been analyzed cytogenetically, and their diploid number varies from 2n♂ = 15 to 2n♂ = 32. The sex chromosome system (SCS) is commonly of the X type, but SCS of the X_1X_2 and X_1X_2Y types were also recorded. The meta/submetacentric morphology of the chromosomes predominates in the species karyotyped (see Oliveira et al. 2007). *Mesabolivar luteus* (Keyserling 1891), a representative of the "miscellaneous group," is the single species of *Mesabolivar* characterized chromosomally and its diploid complement was described as 2n♂ = 15 = 14 + X (Araujo et al. 2005). Considering that *M. brasiliensis* and *M. cyaneotaeniatus* belong to the same *Mesabolivar* operational group, the aim of the present work was to determine and compare the mitotic and meiotic chromosomal characteristics of both species and to discuss the cytogenetic similarities with *M. luteus*, the karyotype of which was previously described by Araujo et al. (2005).

METHODS

Three embryos (one male and two females) and six adults (five males and one female) of *M. brasiliensis* collected at Estação Ecológica de Boracéia (22°11′S, 48°46′W), Salesópolis, state of São Paulo, Brazil and five males (two pre-adults and three adults) of *M. cyaneotaeniatus* collected at Universidade Estadual Paulista (UNESP), Rio Claro (22°41′S, 47°56′W), state of São Paulo, Brazil, were cytogenetically analyzed. The pre-adult and adult specimens were deposited in the collection of Arachnida in the Laboratório de Artrópodes, Instituto Butantan, São Paulo, state of São Paulo, Brazil (IBSP, A.D. Brescovit) (*M. brasiliensis* – IBSP 48221, 48223, 48229, 48234, 48235, 48241; *M. cyaneotaeniatus* – IBSP 75519, 75524, 75511, 75512, 75513).

Embryos and gonads were dissected in insect physiological solution (7.5g NaCl, 2.38g Na_2HPO_4, 2.72g KH_2PO_4 in 1L of distilled water), transferred to colchicine solution (0.05% for embryos and 0.16% for gonads, both in insect physiological solution) and left for 2 h; a volume of hypotonic solution (tap water) equal to that of the colchicine solution was added, and

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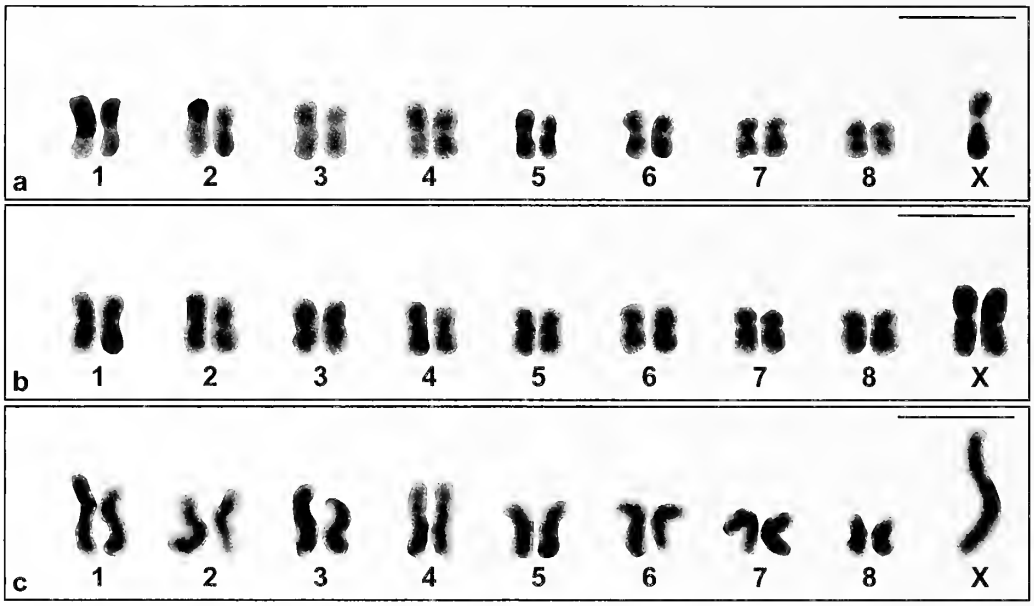

Figure 1.—Karyotypes of the *Mesabolivar* species standard stained with Giemsa: a, b. *Mesabolivar brasiliensis* with $2n♂ = 17 = 16 + X$ and $2n♀ = 18 = 16 + XX$, respectively; c. *Mesabolivar cyaneotaeniatus* with $2n♂ = 17 = 16 + X$. Note that in both species the X sex chromosome is the largest element of the complement. Scale = 10μm.

after 15 min, the material was placed in Carnoy I (3 methanol: 1 acetic acid) fixative solution for 30 min. The material was then transferred to a drop of 60% (embryos) or 45% (gonads) acetic acid on a microscope slide, and the material was macerated to form a cell suspension. The slide was dried on a metal heating plate at 35–40° C and most of them were stained with a 3% Giemsa solution for 13–15 min. Additionally, for detection of the AT- and GC- rich chromatin regions, some chromosomal preparations were stained with the fluorochromes 4′-6-diamidino–2–phenylindole (DAPI) and chromomycin A_3 (CMA_3), and counterstained with distamycin A (DA), according to the technique described by Schweizer (1980). The cells stained with Giemsa were photographed under a Zeiss microscope, using a Kodak Imagelink HQ Microfilm, and those stained with DAPI and CMA_3 fluorochromes were photographed under a Leica fluorescence microscope, using a Kodak T-Max 100 Film. The chromosomal morphology was determined following the nomenclature proposed by Levan et al. (1964).

RESULTS

The analysis of mitotic metaphases of male *M. brasiliensis* and *M. cyaneotaeniatus* revealed the karyotype with $2n = 17 = 16 + X$ (Fig. 1a, c). Only female specimens of *M. brasiliensis* were available for the study and showed a diploid complement of $2n = 18 = 16 + XX$ (Fig. 1b). There were no evident chromosomal size classes. Based on chromosome morphology, the elements of the karyotype were tentatively arranged in pairs in order of decreasing size. In both species, the X chromosome was always easily identified as the largest element of the karyotype (Fig. 1). In *M. brasiliensis*, the chromosomal morphology was established by means of embryo mitotic metaphase chromosomes, and all elements were classified as meta/submetacentric (Fig. 1a, b). In the case of *M. cyaneotaeniatus*, the male mitotic metaphases presented a less condensed condition, becoming impossible to determine the precise position of the centromere in the majority of the chromosomes (Fig. 1c). However, the analysis of metaphase II cells of *M. cyaneotaeniatus* revealed the meta/submetacentric morphology of all chromosomal elements (Fig. 2c, d). No evident secondary constrictions were found in mitotic metaphase chromosomes of either species.

The observation of diplotene eells of *M. brasiliensis* and *M. cyaneotaeniatus* revealed eight autosomal bivalents and one univalent, the X chromosome (8II+X), identified by its large size. In both species, each autosomal bivalent presented only one terminal or interstitial chiasma (Fig. 2a, b). The characteristics shown by diplotene cells of the two *Mesabolivar* species studied here confirmed the diploid number of $2n♂ = 17$ and the SCS of the X/XX type in males and females, respectively. The metaphase II cells of *M. cyaneotaeniatus* exhibited nine and eight chromosomes (Fig. 2c, d). The cells with nine chromosomal elements included the X chromosome ($n = 9 = 8 + X$) that was always easily recognized by its large size and positive heteropycnosis (Fig. 2c); the cells with eight elements ($n = 8$) possessed only autosomes (Fig. 2d). These characteristics indicated the regular and reductional segregation of all chromosomes during anaphase I.

Due to the limited material available, only mitotic metaphases of *M. brasiliensis* were stained with base-specific fluorochromes. Mitotic chromosomes subjected to DAPI appeared to stain homogenously, with no differential bright region. On the other hand, the same chromosomes stained with CMA_3 showed bright fluorescence in the terminal region in the majority of the chromosomes, especially in the elements of pair 2. The X chromosomes were one of the exceptions, without differentially fluorescent regions (Fig. 3).

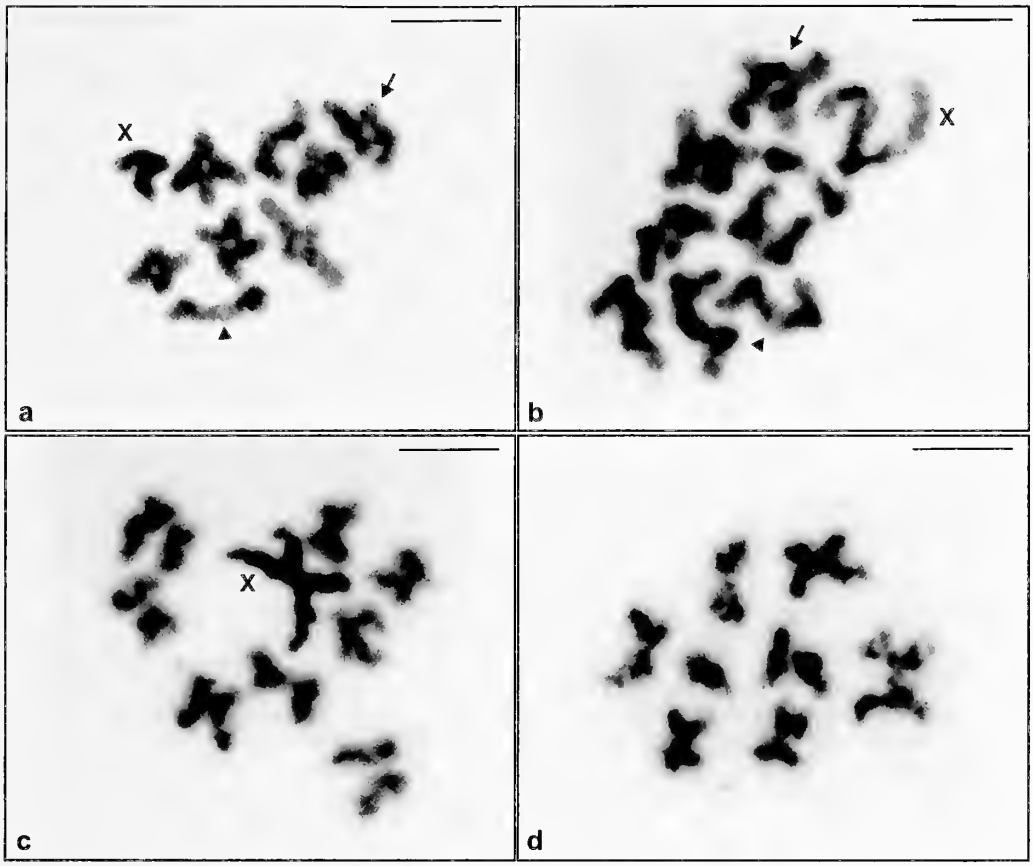

Figure 2.—Testicular meiocytes of the *Mesabolivar* species standard stained with Giemsa: a, b. Diplotenes of *Mesabolivar brasiliensis* and *Mesabolivar cyaneotaeniatus*, respectively, both with 8II + X, exhibiting one interstitial (arrow) or one terminal (arrowhead) chiasma per bivalent; c, d. Metaphases II of *M. cyaneotaeniatus* with n = 9 = 8 + X and n = 8 chromosomes, respectively, revealing that all chromosomes are biarmed. Scale = 10μm.

DISCUSSION

The general chromosomal characteristics of *M. brasiliensis* and *M. cyaneotaeniatus* agree with those found in other pholcid spiders that have been analyzed cytogenetically (see Oliveira et al. 2007). Concerning the diploid number, 2n♂ = 17 was first described for the pholcid *Micropholcus fauroti* (Simon 1887) (Araujo et al. 2005). However, the present addition of two more pholcids with the same number of chromosomes indicates that this diploid number could be as

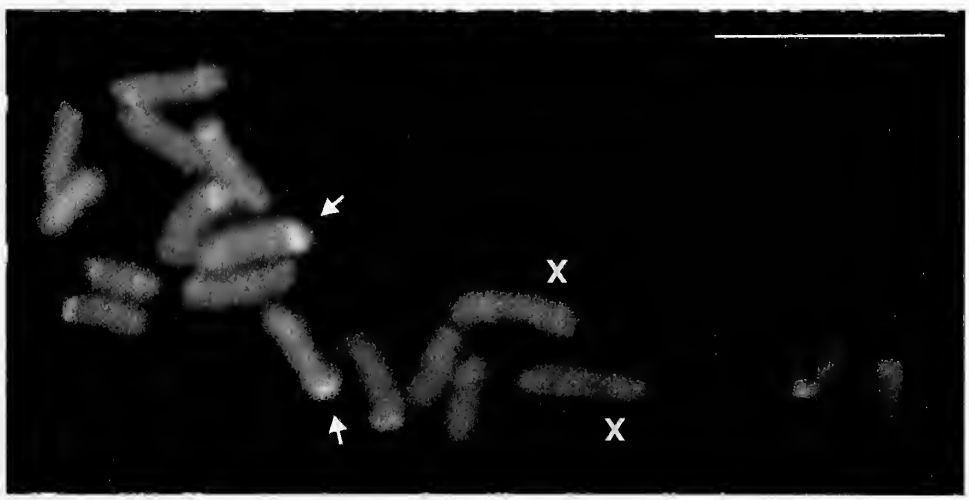

Figure 3.—Mitotic metaphase of *Mesabolivar brasiliensis* with 2n♀ = 18 = 16 + XX stained with CMA_3 GC-specific fluorochrome, showing bright fluorescence in the terminal region of the majority of the autosomes. The arrows indicate prominent GC-rich DNA sequences in the pair 2 chromosomal elements. Scale = 10μm.

widespread as the $2n♂ = 15$, which has been recorded from five species of the family.

With regard to the SCS, the X type in males and XX in females found in both species here studied was also encountered in nine other pholcids (Bole-Gowda 1958; Cokendolpher 1989; Xiuzhen et al. 1997; Araujo et al. 2005; Král et al. 2006; Oliveira et al. 2007), and thus may be the most prevalent form in this family. In species of Pholcidae with X/XX system, the X chromosome seems to be the largest or nearly the largest element of the karyotype. This fact may indicate a single origin of this SCS in this group of spiders. An elegant hypothesis for the origin of the X system from the X_1X_2Y SCS in pholcids was already elaborated by Král et al. (2006).

The meta/submetacentric morphology of the chromosomes found in *M. brasilieusis* and *M. cyaneotaeniatus* agree with that described for the chromosomes of the majority of pholcid species karyotyped thus far, except for acrocentric X chromosomes of *Pholcus crypticoleus* Bösenberg & Strand 1906 (Suzuki 1954) and autosomes of *Pholcus manueli* Gertsch 1937 (under *Pholcus affinis* Schenkel 1953) (Xiuzhen et al. 1997). Suzuki (1954) mentioned that he was able to obtain only a few slides of a quality sufficient to count metaphases and that it was difficult to determine even the chromosome number. It is possible that the morphology of the sex chromosomes has been interpreted incorrectly as acrocentric due to low chromosomal preparation quality. The problem of preparation quality in pholcid cytogenetical research has been highlighted by several authors (see Araujo et al. 2005). As an alternative to describe chromosomal morphology in species of this family, metaphase II chromosomes have been used (Araujo et al. 2005; Král et al. 2006; Oliveira et al. 2007; this work).

Our data from fluorochrome staining are the first from pholcid spiders. Terminal fluorescent regions in chromosomes, such those encountered in *M. brasilieusis*, were observed in species of the genus *Loxosceles* Heineken & Lowe 1832 (Sicariidae Keyserling 1880), other haplogyne species (Araujo pers. comm.).

Our comparison of the karyotype of *M. luteus* obtained by Araujo et al. (2005) with *M. brasiliensis* and *M. cyaneotaeniatus* revealed similar chromosomal morphology with biarmed elements (meta/submetacentrics) and the same SCS of the X/XX type. However, the diploid number differed among these three *Mesabolivar* species, that is, $2n♂ = 15$ in *M. luteus* and $2n♂ = 17$ in both species examined here. Huber (2000) placed *M. brasilieusis* and *M. cyaneotaeniatus* in the same operational group, the "southern group" that includes other species of the genus, and separated *M. luteus* and other *Mesabolivar* species in a "miscellaneous group." The latter group is composed of species that do not fit convincingly into any other genus and is certainly polyphyletic (Huber 2000). A molecular analysis of cytochrome oxidase I gene sequence in pholcids revealed a closer relationship between *M. brasilieusis* and *M. cyaneotaeniatus* than between *M. luteus* and any of these two species (Astrin et al. 2006). The chromosomal results corroborate the idea that *M. brasilieusis* and *M. cyaneotaeniatus* are more closely related to one another than either is to *M. luteus*. The revision by Huber (2000) indicated a probable close relationship between *Mesabolivar luteus* and *Mesabolivar levii* Huber 2000, both belonging to the "miscellaneous group."

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Assessing the conservation value of the spider fauna across the West Palearctic area

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Abstract. Making use of the recent publication of a catalogue of spider species from Europe and the Mediterranean Basin, we built a computer database which indexes all specific and subspecific taxa reported from countries or islands in Platnick's world catalogue as well as in regional or national catalogues. We used this database to analyze the distribution of conservation values at the West Palearctic scale. Three indices of conservation value were calculated and compared between mainland and island territories: species richness, number of endemic species, and I_c, a "Conservation Value Index." Species richness increases with the size of the area being considered, either in islands or in mainland countries, and is highest in Southern Europe. The number of endemics also increases with area, but only for mainland countries, suggesting that different factors determine endemism on islands and in mainland areas. The conservation index shows that several island territories are of a high conservation interest: the Mediterranean and Atlantic islands clearly exhibit the highest conservation value and some islands (mainly Canary and Balearic islands) can be considered hotspots of biodiversity for the West Palearctic area; other hotspots are some small Mediterranean islands.

Keywords: Species richness, endemic species, island theory, Araneae, Europe

The identification of priority areas for species/habitat conservation should first incorporate an evaluation of narrow range species or endemic species to the total species richness. Concerning spiders, a large number of endemic (rare) species have been described and studied in the famous biodiversity hotspot archipelagoes or islands of the Pacific (see for instance Baert et al. 1991; Gillespie 2002; Wood et al. 2007). In contrast, very few studies have dealt with spider rarity in northern areas. Distinct centers of endemism have been pointed out in mainland West Palearctic areas (Deltshev 1999; Marusik & Koponen 2002) and in some Atlantic archipelagoes (Borges & Brown 1999; Arnedo et al. 2001) but very few studies have been made to estimate the global rarity of faunas at national (Ruzcika & Bohac 1994; Gadjos & Sloboda 1995) or local scales (e.g., Pétillon et al. 2007). Thus, in spite of the presence of spiders in all biota, we have no overview of the distribution of narrow range spider species in the European fauna, which is needed as basic knowledge for European conservation plans (as for instance the so-called "European framework for environmental protection," Natura 2000). Relatively extensive data on the distribution of spiders in Europe and North Africa are now available and stored in a database (Canard 2005). In this study we propose to use these data to determine the distribution of conservation value across the West Palearctic area at a national scale for both mainland and island territories.

The assessment of conservation value is usually based on species richness and rarity. In Europe, rarity status for spiders is currently unavailable or inaccurately estimated. Instead, we used the number of endemic species and a synthetic index based on the integration of degrees of rarity of all species of a territory (Canard & Ysnel 2002). The distribution of these indices were i) analyzed in relation to area of the territory and its location (i.e., geographical sectors, see Methods for details) and ii) compared between islands and mainland territories. Since species richness and the number of endemic species are expected to increase with the size of the area being sampled (MacArthur & Wilson 1967; Emerson & Kolm 2005), these two parameters were analyzed by accounting for the area effect. That also allows us to explore the robustness of the database.

METHODS

The European reference database is stored on an Access database (not yet available on the Internet, but available from the authors on request). Following Canard (2005), the West Palearctic zone is divided into six different sectors (Table 1): North and Far East Europe, Atlantic Europe, Central Europe, Mediterrancan Europe, Mediterranean Middle East, and North Africa and South Atlantic islands. Spider occurrence data for these sectors come from Canard's Catalogue (Canard 2005) updated with Platniek's World Spider Catalog data (Platniek 2007) and with national checklists published or available on the Internet (see Table 2). Before being integrated in the reference base, data from the Internet were critically analyzed and, in case of doubtful mentions, the relevant species were not included in the database. At the moment the database lists 5,603 species (presence /absence data) from 75 territories (49 mainland countries and 26 islands).

For each territory, species richness, number of endemic species, Conservation Value Index (I_c, see details below) and surface area were determined (Table 1). In order to respect normality, the data were log(x + 1)-transformed. ANCOVAs were carried-out on species richness and number of endemic species with "insularity factor" (island vs. mainland) as categorical fixed factor and territory area as continuous covariate (Model 1; Gareía-Berthou 2001). If the covariate-by-factor interaction was not significant (homogeneity of slopes), a Model 2 (standard ANCOVA) was performed. If the interaction was significant, the data from both types of territories (island and mainland) were separately analyzed with respect to their area (standard linear regression analysis: Model 3).

Evaluating conservation value through the global range of rarity of spider faunas makes sense because a country colonized mainly by ubiquitous species (with high dispersal abilities and a broad ecological spectrum) has a low arachnological conservation value. On the other hand, a country having many rare specialized species (endemic and/or stenotopic species, with a narrow geographical and/or ecological spectrum) may have a high conservation value. Referring to this idea, a "Conservation Value Index" (I_c) based on the relative rarity of spider species was elaborated to estimate the conservation value of the different communities of each territory (islands and mainland countries) of the West Palearctic area. This index is the same that we have earlier described under the name of "patrimonial index" (Canard & Ysnel 2002). Fig. 1 gives a theoretical example showing how I_c is calculated. The calculation consists of ordering the number of species collected for all the spiders of West Palaearctic (Z1) and in the territory tested (Z2) according to the different numbers of stations known for each species. These numbers are calculated as percentages

Table 1.—Biogeographic sector, name of the country/island, code (C), insularity factor (I, Ma = Mainland, Is = Island, area (A, km^2), number of endemic species (Ne), speeies riehness (S), and Conservation Value Index (I_c). Countries are coded according to the ISO 3166-1-alpha-2 A norm except for United Kingdom which was divided into Great Britain (GB) and Ireland s.l. (including Northern Ireland, coded IR). All islands, constituting a country or not, were coded separately by the first two letters of their names (as far as possible). x: Ic not calculated.

Sector	Namc	C	1	A	Ne	S	I_c
North and Far East Europe							
1	Estonia	EE	Ma	45226	3	514	−55.70
1	External Hebrides	HE	Is	3071	0	147	−56.80
1	Finland	FI	Ma	338145	6	629	−52.30
1	Iceland	IS	Is	103125	2	111	−51.80
1	Jan Mayen	JA	Is	377	0	5	x
1	Latvia	LV	Ma	64589	0	439	−56.90
1	Lithuania	LT	Ma	65303	1	48	−57.40
1	Norway	NO	Ma	324220	3	558	−54.40
1	Russia	RU	Ma	17075400	90	1247	−37.40
1	Svalbard	SV	Is	61606	1	20	x
1	Sweden	SE	Ma	449964	2	702	−53.08
Atlantic Europe							
2	Belgium	BE	Ma	30528	1	702	−55.20
2	Faroe Islands	FE	Is	1399	0	39	−56.00
2	France	FR	Ma	675417	190	1507	−36.34
2	Great Britain	GB	Is	229850	2	636	−55.10
2	Ireland	IR	Is	84431	0	415	−56.40
2	Isle of Man	IM	Is	572	0	194	−57.20
2	Netherlands	NL	Ma	41526	0	623	−55.07
2	Orkney Islands	OR	Is	990	0	130	−56.80
2	Shetlands Islands	SH	Is	1426	0	81	−56.70
Central Europe							
3	Austria	AT	Ma	83858	14	982	−49.50
3	Belarus	BY	Ma	207600	0	387	−57.10
3	Bulgaria	BG	Ma	110910	37	981	−48.30
3	Czeeh Republic	CZ	Ma	78866	1	841	−53.87
3	Denmark	DK	Ma	43094	1	530	−56.40
3	Germany	DE	Ma	357027	3	1005	−51.80
3	Hungary	HU	Ma	93030	6	726	−54.60
3	Luxembourg	LU	Ma	2586	0	48	−57.40
3	Macedonia	MK	Ma	25713	10	440	−52.03
3	Moldavia	MD	Ma	33843	0	291	−55.90
3	Poland	PL	Ma	312685	1	774	−54.35
3	Romania	RO	Ma	238391	53	960	−48.06
3	Serbia	RS	Ma	88361	31	623	−54.50
3	Slovakia	SK	Ma	48845	4	902	−53.10
3	Switzerland	CH	Ma	41285	4	944	−52.06
3	Ukraine	UA	Ma	603700	28	833	−50.11
Mediterranean Europe							
4	Aegean Islands	IE	Is	4395	7	97	−45.10
4	Albania	AL	Ma	28748	2	29	−44.80
4	Balearic Isles	BL	Is	4992	31	59	3.90
4	Bosnia	BA	Ma	51130	23	65	−14.41
4	Corsica	CO	Is	8569	35	512	−43.50
4	Crete	CR	Is	8336	58	284	−30.17
4	Croatia	HR	Ma	56542	36	630	−47.50
4	Cyclad Islands	CC	Is	2630	8	148	−45.50
4	Dodecanese Islands	DO	Is	2564	15	284	−45.80
4	Greece	GR	Ma	131940	61	629	−40.70
4	Ionian Islands	IO	Is	2370	19	227	−43.44
4	Italy	IT	Ma	301230	149	1183	−39.70
4	Malta	MT	Is	316	7	11	x
4	Montenegro	ME	Ma	13812	0	11	x
4	Portugal	PT	Ma	88800	24	702	−43.60
4	Sardinia	SR	Is	3	1	205	−42.90
4	Sicily	SC	Is	25700	26	242	−42.02
4	Slovenia	SI	Ma	20270	15	514	−53.10

Table 1.—Continued.

Sector	Name	C	I	A	Ne	S	I_c
4	Spain	ES	Ma	504782	122	1177	−37.86
4	Sporad Islands	SP	Is	414	0	25	−55.11
Mediterranean Middle East							
5	Armenia	AM	Ma	29800	0	149	−47.90
5	Azerbaijan	AZ	Ma	86100	55	624	−38.26
5	Cyprus	CY	Is	9251	9	47	−24.60
5	Georgia	GE	Ma	69700	48	493	−40.06
5	Israel	IL	Ma	20770	134	459	−12.70
5	Jordan	JO	Ma	92300	0	6	
5	Lebanon	LB	Ma	10452	16	186	−50.40
5	Syria	SY	Ma	185180	16	261	−37.31
5	Turkey	TR	Ma	779452	99	528	−38.10
North Africa and South Atlantic Islands							
6	Algeria	DZ	Ma	2381741	243	717	−12.47
6	Azores	AC	Is	2333	17	89	−30.60
6	Canary Islands	CA	Is	7447	299	411	19.50
6	Egypt	EG	Ma	1001449	19	365	−25.27
6	Libya	LY	Ma	1759540	55	451	−56.70
6	Madeira	MR	Is	779	54	171	−14.50
6	Salvage Islands	SA	Is	24090	31	4	x
6	Tunisia	TN	Ma	163610	33	351	−35.14
6	Morocco	MA	Ma	446550	112	321	−11.03

relative to the total numbers. The Conservation Value Index sums these values over the occurrence classes as:

$$I_c = \sum (Z2 - Z1)/Q$$

where Q is the mean number of stations for the class being considered (i.e., midpoint of the interval).

The index is calculated in an Access program. Referring to the actual database, the Conservation Value Index may vary from a strong negative value when there are only very common species in the country investigated (I_c min) to a high positive value when there are only rare species in the fauna investigated (I_c max). We calculated the upper and the lowest values of Ic by testing lists of species all of which were known from only one country (I_c max = +39.6) or all known from more than 40 countries in the database (I_c min = −58.0). Another noticeable value is « zero » which corresponds to a theoretical community composed of all the species of the reference base or a smaller number of species distributed in the same way over the occurrence classes. It must be underlined that the index is very sensitive to the presence/absence, and to the number of species collected (Canard & Ysnel 2002). Thus, comparisons have to be made for communities or faunas of similar specific richness, especially for assemblages composed of less than 50 species. No species is found in all the 75 territories investigated and the reference curve shows that almost 50% of the species in the database are found in only one country or island (Fig. 1).

RESULTS

The size of the area has a significant positive effect on species richness for both island and mainland territories (Fig. 2) and insularity does not influence this relationship (Table 3). Area as well as the interaction area × insularity factor has a significant effect on the number of endemic species per territory. When considering islands and mainland areas separately, the number of endemic species is positively and significantly influenced by the area only for mainland areas (Fig. 3), whereas the number of endemic species does not vary significantly with the size of the area for islands (Table 3).

Fig. 4 shows the different values of the Conservation Value Index according to the specific richness of the different biogeographic sectors. I_c was calculated for the summed lists for islands/mainland countries of each sector. The differences observed between the I_c values of each sector reflect a difference in spider distribution between sectors and clearly separate the six sectors according to their conservation values. Low conservation values concern continental territories of Central Europe (Ma3: I_c = −41.2; 1583 spp.), islands territories of both North and Far Eastern Europe (Is1: I_c = −52.2; 212 spp.), and Atlantic Europe (Is2: I_c = −54.8; 647 spp.). The highest conservation value for continental areas is from North Africa (I_c = −6.4; 1292 spp.) and for the South Atlantic islands (I_c = +7.3; 846 spp.). The species richness of Mediterranean Europe (Sector 4) is high, and its I_c value is higher than those of Central or Northern mainland sectors. Within this sector, Bosnia exhibits a high conservation value. Several mainland countries of sectors 5 (Israel and Lebanon) and 6 (Algeria, Egypt, Morocco as well as Madera Islands to a lesser extent) are of particular interest in term of global rarity of the spider fauna. Canary Islands and Madeira Islands exhibit the highest level of endemic species across the West Palearctic, contributing to the high percentage of species known from only one territory (see I_c values in Table 1).

DISCUSSION

By using the available data on spider distribution, the relationship between area and species richness is shown for both islands and mainland countries. This result is consistent with several previous studies and the Island theory, therefore, applies for spiders at the West Palearctic scale. The number of endemic species increases with the size of the area only for mainland countries. That may reflect the fact that the larger the country is, the higher the number of habitats, each one being likely to produce specialized endemic species. Surprisingly, we did not find this relationship for islands. Thus, other parameters – such as temporal and/or spatial isolation – could determine the high insular endemic rates in some Southern-European islands (Emerson & Kolm 2005).

Table 2.—National checklists integrated to the database for updating Canard (2005) and Platnick (2007) catalogues.

Sector	References
North and Far East Europe	Aakra & Hauge 2003 Agnarsson 1996 Koponen 2005 Kronestedt 2001 Logunov & Marusik 2003 Mikhailov 1997, 1998a,b,c. Relys & Spungis 2004 Scharff & Gudik-Sorensen 2006 Tanasevitch 2004 Vilkas 2004
Atlantic Europe	Bosmans& Vanuytven 2004 Le Péru 2007 Merrett & Murphy 2000 Van Helsdingen 2006 Vanuytven 2006
Central Europe	Blagoev 2002, 2005 Blagoev et al. 2005 Blick et al. 2004 Buchar & Ruzicka 2002 Deltshev et al. 2003 Gajdos et al. 1999 Klimeš 2006 Kritscher 1996 Samu & Szinetár 1999 Weiss & Urák 2000
Mediterranean Europe	Alicata & Cantarella 2004 Bosmans & Chatzaki 2005 Cantarella 1982 Cardoso 2005 Milosevic 2002 Morano 2007 Pesarini 1995, 2003 Van Helsdingen 2005
Mediterranean Middle East	Amr 2003 Topcu et al. 2005 Varol 2003
North Africa and South Atlantic Islands	El-Hennawy 2006

The index of conservation value has been previously used to compare the conservation value of different habitats at a regional scale (Canard et al. 1998; Canard & Ysnel 2002). When comparing the global rarity of spider faunas at the European level using numerous datasets, this calculation helps to quickly focus on specific biogeographic or political areas. As shown by increasing I_c values from the northern to the southern areas, narrow-range spiders are more likely to be found in the south of the West Palearctic area. Due to the increasing number of new species descriptions during the last deeades, the present study reveals a particularly high level of endemism in the Canary Islands eompared to other sectors. Although the spider fauna of Madeira Islands is still poorly described, we also found an unexpected high level of endemism. The Mediterranean basin - including the Atlantic islands - is home to numerous endemie plants, insects, or reptiles and no less than ten specific regional hotspots have been idcntified in North African territories and Mediterranean or Atlantic islands (Medail & Quezel 1999). Considering this first approach to examine the conservation values of various European spider faunas, it may be assumed that these hotspots are likely to be priority sites for spider conservation. In the future, special attention must be paid to the spider fauna of the southern islands,

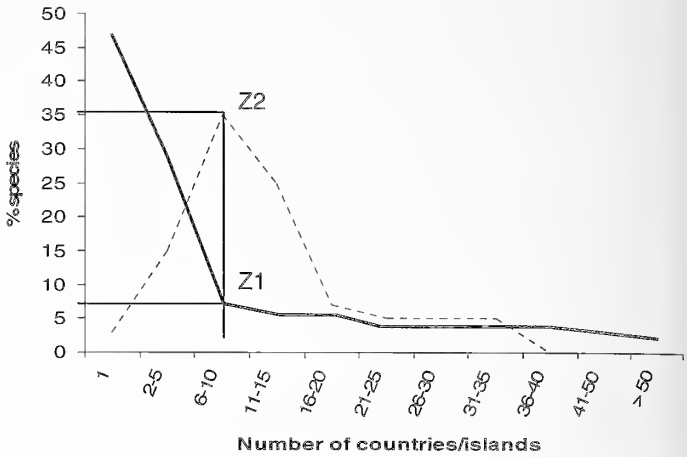

Figure 1.—Comparison between the curve based on the referenee data base (solid line) and a curve based on an investigated territory (dotted line). At point Z1 there are 6% of the total speeies of the reference base known from 6 to 10 countries. At point Z2, there are 35% of the species in the territory investigated known from 6 to 10 countries in the reference base. The conservation value index (I_c) is calculated by summing up the differences between Z1 and Z2 over all x-axis groups.

especially to mini-hotspots as for instanee Madeira, Salvage, and Balearic islands, which are notably under-sampled.

The proportion of endemic species is low in Central European countries, indicating that these countries are dominated by widespread species. Particularly high conservation indices in mainland countries such as Bosnia and to a lesser extent Russia refleet the occurrence of specialized species assoeiated with particular relatively isolated habitats (e.g., eaves or high mountains, Deltshev 1999), or reflect their glaciation history (Marusik & Koponen 2002). Furthermore, at the seale we investigated, the presence of biogeographic crossroads (sensu Spector 2002) for spiders may also lead to low I_c values by increasing the number of species shared with other countries. Further studies should thus analyze the contribution of different climatic regions or eco-regions within countries, notably large and recognized biogeographic crossroad areas such as Russia, France, or Spain. Sueh large-scale data have inherent shortcomings due to possible variation in sampling intensity between territories Therefore, though large differences between I_c values may indicate

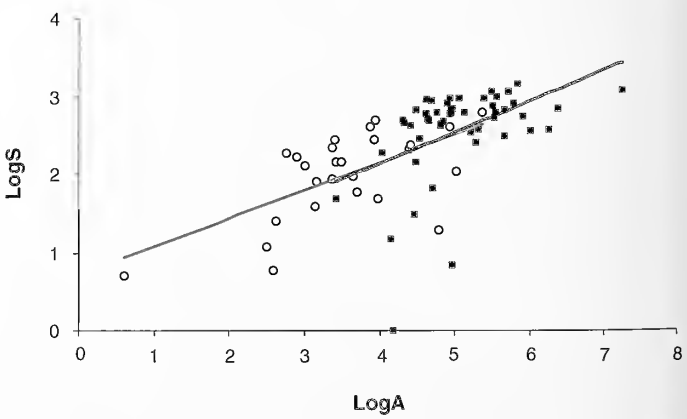

Figure 2.—Relationship between speeies riehness (logS) and the size of the area (logA, km^2) in mainland (black squares) and island (open eireles) territories. Black and grey lines: linear regressions for mainland countries (LogS = 0.539 + 0.403 LogA) and islands (LogS = 0.723 + 0.360 LogA).

Table 3.—Influence of the size of the area (continuous predictor, logA) and insularity (discontinuous factor, Is: island, Ma: mainland) on species richness and the number of endemic species. For details on statistical analysis, see Methods.

		d.f.	*F*-ratio	R^2 adjust.	*P*
Species Richness					
Model 1	Whole	71	15.52	0.371	**<0.0001**
	Insularity	1	0.07		0.7873
	LogA	1	25.42		**<0.0001**
	Insularity *LogA	1	0.08		0.7772
Model 2	Whole	72	23.54	0.387	**<0.0001**
	Insularity	1	<0.01		0.9870
	LogA	1	25.68		**<0.0001**
Number of endemic species					
Model 1	Whole	71	6.65	0.186	**<0.0001**
	Insularity	1	6.33		**0.0141**
	LogA	1	13.67		**<0.0001**
	Insularity *LogA	1	4.98		**0.0288**
Model 3	LogA(Is)	24	0.97	−0.001	0.3334
Model 3′	LogA(Ma)	47	18.31	0.265	**<0.0001**

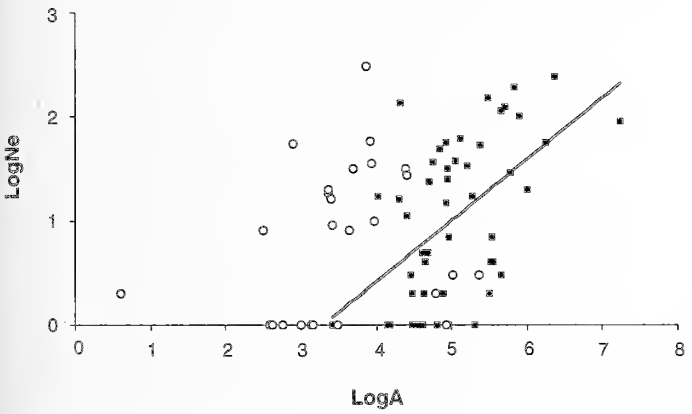

Figure 3.—Relationship between number of endemic species (logNe) and the size of the area (logA, km^2) in mainland (black squares) and island (open circles) territories. Black line: linear regression for mainland countries (LogNe = 0.588 LogA − 1.94).

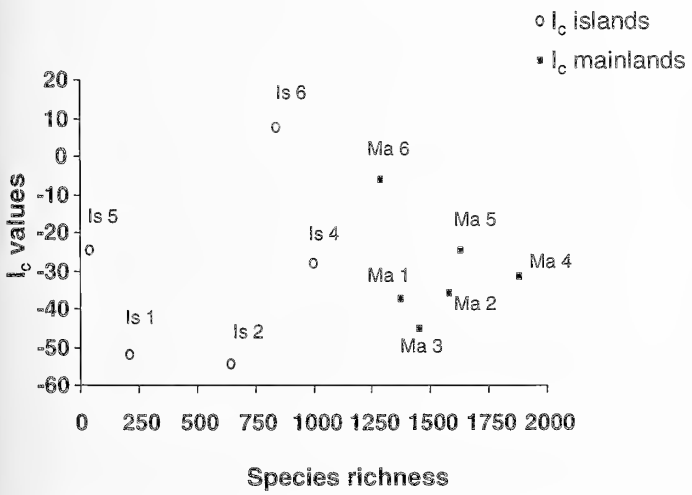

Figure 4.—Species richness and conservation value index of islands (Is, open circles) and mainland countries (Ma, black squares) belonging to the different biogeographic sectors of the West Palearctic area (Sector codes: see the Table 1).

real differences in originality of spider faunas, small differences cannot at the moment be reliably interpreted.

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SHORT COMMUNICATION

Relationship between litter characteristics and female size in *Tityus stigmurus* (Scorpiones, Buthidae)

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Abstract. *Tityus stigmurus* (Thorell 1876) is one of the most medically important scorpion species in Brazil, but many basic aspects of its life history are unknown. Here the pattern of female reproductive investment was examined, along with development of the 1st and 2nd instars and the relationship between 2nd instar mass and molting to the 3rd instar. Relative to other buthid scorpions, *T. stigmurus* has a smaller litter (average 10 young) and a shorter 1st-instar period (average 4 days) and 2nd-instar period (average 68 days). Neither litter size nor offspring mass showed a relationship to female size. A significant positive correlation was observed between total litter mass and litter size. The minimum mass required for successful molting to the 3rd instar was 34.0 mg. Overall, female reproductive resources in *T. stigmurus* appear to be applied to the production of more but not heavier offspring.

Keywords: Litter size, female size, reproductive investment, offspring mass, intermolt period

Differences in female reproductive investment are common in closely related species of animals. A female may use her finite reproductive resources to maximize her fitness by producing either large litters of small young or small litters of large young. Given that the individual fitness of each offspring is generally correlated with larger maternal investment, the female's option of producing large litters with small young creates a potential conflict in the fitness of the female and her young. Thus, the optimal distribution of parental resources tends to be based on the cost-benefit relation for both parents and offspring (Smith & Fretwell 1974; Stearns 1992; Fox & Czesak 2000).

In scorpions, studies on the female reproductive investment are still scarce, yet such studies have shown that different taxa show different tendencies. In species such as *Centruroides exilicauda* (Wood 1863), *Vaejovis spinigerus* (Wood 1863), *Diplocentrus peloncillensis* Francke 1975, and *Pseudouroctonus apacheanus* (Gertsch & Soleglad 1972) there is no relationship between female size and offspring production (Brown 2004). However, a higher reproductive investment in larger litters was recorded in the largest females in *Centruroides vittatus* (Say 1821), *Vaejovis spinigerus* (Wood 1863), and *Tityus columbianus* (Thorell 1876) (Formanowicz & Schaffer 1993; Lourenço et al. 1996; Brown 2004). Although *Tityus* species are capable of producing multiple litters from a single insemination (Kovoor et al. 1987; Polis & Sissom 1990; Lourenço et al. 1996), little is known about female reproductive investment, including species involved in medically important envenomations in Brazil.

Population dynamics are also influenced by the duration of postembryonic development. Within Buthidae, this varies from six to 48 months depending on the species (Polis & Sissom 1990). Both female reproductive investment and postembryonic duration are unknown for *Tityus stigmurus* (Thorell 1876), a species that is widely distributed in urban areas of northeastern Brazil and responsible for many reported envenomations each year (Eickstedt 1983, 1984; Lira-da-Silva et al. 2000; Barbosa et al. 2003). Its occurrence in urban settings reflects its ability to live under roofs, among accumulated debris in the exterior areas of residences (Eickstedt 1983, 1984; Lourenço et al. 1996), and in cesspits.

This study analyzed the litter size, offspring mass, and total litter mass of *T. stigmurus* and evaluated the relation of female size to these variables. Times of development for 1st and 2nd instars, as well as the relationship between mass and molting to the 3nd developmental instar, were also assessed.

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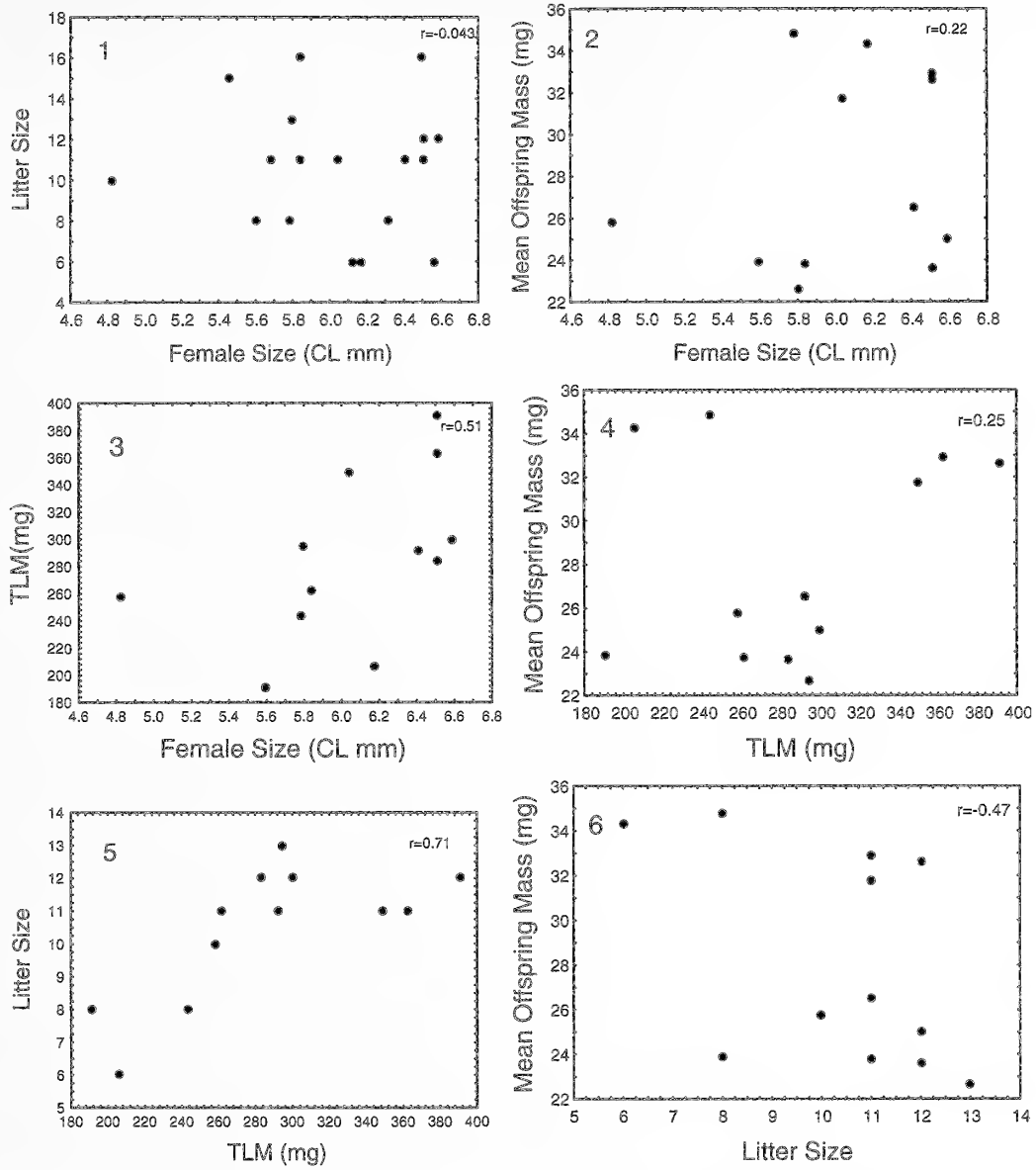
METHODS

Animal sampling and maintenance.—*Tityus stigmurus* adults were collected from residential areas of Recife (8°04′03″S, 34°55′00″W), Pernambuco State. The climate is predominantly hot and wet with mean temperature 25° ± 2° C and annual pluviometric precipitation of 2.094 mm. Following capture, animals were individually housed in plastic terraria (8.5 cm diameter × 7.8 cm height) where water and shelter were made available. Weekly, *Periplaneta americana* (Linnaeus 1758) nymphs were offered as food. The animals were kept at 28° ± 3°C mean temperature and 12:12 h light/dark photoperiod.

Data collection and analysis.—The relationship between maternal carapace length (CL) and litter size (LT) was analyzed in a sample of 25 pregnant females that gave birth to young. In 14 broods, it was possible to analyze 1st instar duration and to determine total litter mass (TLM) and mean offspring mass (MOM). TLM was taken as a measure of reproductive investment and was calculated as the sum of individual masses of juveniles according to the methodology of Brown (2004). Juveniles were weighed to the nearest 0.1 mg with an analytical balance (Mettler AE 260 DeltaRange) as soon as they moved down from the mother's dorsum. After offspring dispersal, female CL was measured with digital calipers to the nearest 0.1 mm under a dissecting microscope (Leica MZ6).

Litter size was estimated by counting juveniles on the female's dorsum within 24 h of birth and again immediately after dispersal. All dead and living juveniles were counted except for those cannibalized. Due to a female's habit of cannibalizing young at birth and the superimposed distribution of young on her dorsum, an accurate litter size was difficult to obtain. Eight gravid females were dissected and the number of young recorded for litter size comparison. Females chosen for dissection showed signs of imminent parturition such as lack of movement and an enlarged mesosoma with offspring visible through the integument. In general, females presenting these traits gave birth within two weeks.

ANOVA was used to test the differences between brood sizes. The correlation coefficient (Pearson's r) was used to evaluate the relationships between female CL and litter size, mean offspring mass or TLM. It was also used to examine the relationship between TLM and litter size or MOM. The significance of these correlations was assessed with a t-test.



Figures 1–6.—Correlation results between carapace length (CL) and brood characteristics of *Tityus stigmurus*. 1. Litter size (LT); 2. Mean offspring mass (MOM) 3. Total litter mass (TLM); 4. Correlation between total litter mass and mean offspring mass. 5, 6. Correlation between total litter mass (TLM) against litter size and litter size, respectively, with mean offspring mass in *Tityus stigmurus*.

Duration of first and second instars and mass variation in the latter.— The duration of the 1st instar stage was determined for 25 litters by counting the days between birth and the first molt. A second sample of 19 newly dispersed individuals was used to determine the period between the 1st and 2nd molts. Between molts, the animals were fed weekly with nymphs of *P. americana* with mean mass of 7.8 mg. Masses of 2nd instars were determined 24 h after each feeding in order to estimate variation in mass and to determine any relationship between mass and molting. The difference between the initial mass (Mi), recorded up to 24 h after dispersal, and the final mass (Mf), recorded immediately prior to the 2nd molt, was used as an estimate for the mass variation in the 2nd instar. The lowest Mf was used as an estimate of the minimum mass needed to molt successfully.

RESULTS

Tityus stigmurus showed great variation in female size, litter size, and mean offspring mass. Female size (CL) averaged 6.00 ± 0.44 mm, varying from 4.82 to 6.59 mm. The litter size (LS, n = 25 females) averaged 10.40 ± 2.90 and was unrelated to female size (Fig. 1). Similar data were obtained in the group used to analyze total litter mass (TLM) and mean offspring mass (MOM) (n = 14 females) (CL = 6.03 ± 0.48 mm and LS = 10.14 ± 2.11, respectively). MOM in this group averaged 27.67 ± 4.8 mg and was not related to female size (Fig. 2). The mean brood size obtained from females dissected before parturition (n = 8; 11.87 ± 4.09; range 8–21) was not significantly different from those that gave birth to live young ($F_{(0.05;1;23)} = 0.62$; $P = 0.55$).

The reproductive investment (TLM) showed a positive, but not significant, correlation with female size (Fig. 3) and mean offspring mass (Fig. 4). However, a significant positive correlation was found between TLM and litter size (Fig. 5). A negative but not significant correlation was found between litter size and mean offspring mass (Fig. 6).

Female mass before parturition (until after the last feeding) ranged from 975.4 to 1655.0 mg, showing a TLM-to-female-mass ratio higher than 0.20 for most females (n = 9/12, ranging from 0.13 to 0.42).

Table 1.—Data on reproductive investment and first instar traits of 12 broods of *Tityus stigmurus*. CL = maternal carapace length.

CL (mm)	Litter size	1st instar Period (days)	Mean offspring mass (mg)	Total litter mass (mg)
6.41	11	4	26.5 ± 1.7	292.0
5.84	11	5	23.8 ± 3.2	261.4
6.17	6	4	34.3 ± 3.0	205.9
6.51	12	4	23.6 ± 1.0	283.7
4.82	10	3	25.8 ± 2.6	257.8
6.51	11	5	32.9 ± 4.1	362.3
6.51	12	5	32.6 ± 3.0	391.5
6.04	11	3	31.7 ± 3.1	349.3
5.60	8	4	23.9 ± 2.1	190.9
5.78	8	4	34.1 ± 3.0	272.6
6.59	12	3	25.0 ± 0.5	299.7
5.80	13	7	22.7 ± 1.6	294.4
6.02	10	3	29.9 ± 2.73	298.8
5.81	7	3	24.1 ± 3.08	168.6

Birth, first instar and pre-dispersal phase.—The duration of the first instar was investigated in a sample of 142 individuals from different litters. This period was on average 4.07 ± 1.14 days (range 3–7) (Table 1) and the molt occurred simultaneously in offspring of the same litter. After the first molt the immature individuals remained on the mothers dorsum for 5–6 more days. Dispersal occurred 5–10 days following birth. Individual young occasionally climbed down from the female's dorsum, particularly in the nocturnal period, then returned to the mother. While off the female, they searched for water and food in the environment. After the transition period from dorsum to the environment, they remained apart from the mother, though aggregated in the shelters placed in the terraria.

Second instar phase.—The intermolt period between the 2nd and 3rd instar ($n = 19$) was approximately 16 times longer than the duration of the 1st instar. The simultaneity observed in the first molt did not occur in the second, and the duration of this phase of development was on average 67.81 ± 18.80 days (ranging = 42–107 days). The mortality for the 2nd instar was 47.37%, and among these 33.33% died during the intermolt period (one due to cannibalism) and 66.67% died during the molting process (Table 2). No relationship was observed between mass of the offspring before a molt and survival during the molt. The minimal pre-molt mass of a surviving individual was 34.0 mg and the maximum was 59.0 mg. However, many immatures with masses ranging between 49.0 mg and 56.0 mg died during or after the molt.

DISCUSSION

Tityus stigmurus can vary greatly in female size, litter size, mean offspring size, and total litter mass, as described for other scorpion species both within and among populations (Brown 2001, 2003). These traits are important components of female reproductive investment, and impact the fitness of both the female and her offspring.

Based on data summarized by Polis & Sissom (1990) and Lourenço (2007), *T. stigmurus* had lower brood sizes (mean of 10 young) compared to most buthid species (average 32) and other species of *Tityus* (mean variation = 15–25). Our results show that females that allocated more resources to reproduction (measured as TLM) had more but not heavier offspring, and that TLM was not significantly related to female size (CL). This may explain the lack of correlation between CL and litter size. There are few studies on the reproductive investment in *Tityus* species, although Lourenço et al. (1996) found a positive correlation between litter size and female size in both parthenogenetic and sexual populations of *T. columbianus*. It is important to note that our study used females that had been maintained in the laboratory for at least a year and that data such as prey availability and specimen age were not controlled. Thus, variation in prey availability in the environment may have led to differential resource allocation by females resulting in large variation in TLM. A shift in offspring size from negative to positive values in *V. vorhiesi* Stahnke 1940 was attributed to an increase in prey availability in the environment, which allowed females to invest more in reproduction (Brown 2001). In addition, old females tend to reduce the number of follicles (Lourenço 1979) which may lead to small litter sizes. Therefore, lack of correlation between most of our variables may have been influenced by factors such as accessibility of food in the environment and the age of females.

Table 2.—Development length (days) and mortality rates in *Tityus stigmurus* 2nd instar.

Litter size	Second instar period, mean ± SD (range)	Mortality (%)
7	72.2 ± 22.70 (52–107)	85.71
2	64.5 ± 20.51 (50–79)	0
1	56	0
8	69.12 ± 17.00 (50–95)	25.00
1	42	100
19	67.81 ± 18.80	47.37

In contrast, in several species such as *Centruroides exilicauda*, *Vaejovis spinigerus*, *Diplocentrus peloncilleusis*, *Pseudouroctonus apacheanus* (Brown 2004) and *Centruroides vittatus* (Formanowicz & Shaffer 1993), larger females invest more in reproduction. In these species, a positive correlation between female size and total litter mass has been described. Moreover, litter size was often positively related with CL and TLM, showing that the largest females invest more in reproduction through production of more offspring. In all of these speeies, as well as in *T. stigmurus*, there was no correlation between female size and mean offspring mass, indicating that larger females do not produce larger offspring. Offspring mass in *T. stigmurus* was also not correlated with litter size, which may suggest a lack of trade-off between mass and number of individuals. Similar results were obtained by Salomon et al. (2005) in the spider *Stegodyphus lineatus* Latreille 1817. Offspring mass in this spider showed no correlation with clutch size, indicating that each variable may be determined independently. In addition, offspring mass at hatching (and consequently egg size) appeared to be relatively constant and independent of female size and body mass.

In all of the observed litters, juveniles remained unfed on the mother's dorsum during the entire 1st instar phase and underwent the 1st ecdysis simultaneously, a phenomenon characteristic of many scorpion species (Sissom & Francke 1983; Polis & Sissom 1990; Brown 1997, 2004; Lourenço 2000; Farley 2005; Lourenço & Goodman 2006). Mean first-instar duration in *T. stigmurus* (4 days) was shorter than other Buthidae, including *Centruroides gracilis*

(Latreille 1804) at 8 days (Francke & Jones 1982), *Centruroides exilicauda* (Wood 1863) (= *C. sculpturatus*) at 7 days (Brown 2004), and *Grosphus hirtus* Kraepelin 1901 at 14 days (Lourenço & Goodman 2006). The first-instar period in *T. stigmurus* is even shorter than that of congeneric species (Polis & Sisson 1990).

Similarly, the 2nd instar of *T. stigmurus* lasted 67 days on average, which was shorter than in other species of Buthidae. Toscano-Gadea (2004) confirmed 321 days for *T. trivittatus*, and Lourenço & Goodman (2006) described a 112 day period for *G. hirtus*. A longer developmental period for *T. stigmurus* was described by Matthiesen (1971), who found an average of 80 and 148 days in two broods of five young each produced by a single female. Scorpions from both studies are likely to have come from different populations since they were obtained from cities separated by 209 km. According to Brown & Formanowicz (1995), individuals from different populations may face an adaptation to microvariation in the environment, and this fact may reflect genetic differences that might explain the differences relative to our findings.

Mortality in the period between the 2nd and 3rd stages was high, as only 52.63% of the initial sample survived. Most of these deaths, 66.67%, occurred during ecdysis, and the body mass at the end of the 2nd stage was not associated with the survival of juveniles. In their experiments with *Vaejovis bilineatus* Pocock 1898, Sissom & Francke (1983) noted that only 43% of the initial sample survived the 2nd molt and suggested dehydration as a possible cause. *Tityus stigmurus* young also appeared to be desiccated after dying during molting, with the integument being dried and frail.

In total, the data gathered in this study suggest that female *T. stigmurus* make a significant investment in reproduction (over 20% of the body mass). It is important to note that the allocation is underestimated given that the neonate scorpions decrease in mass during the first instar period and their first molt (Polis & Sissom 1990). With larger investments in reproduction, there is a trend toward increasing the number but not mass of offspring. Moreover, this trait is not influenced by the mothers size, so that faetors such as age of the female and food availability in the environment are likely to have fundamental importance in the reproductive investment made by this scorpion species. The comparatively short developmental period of this species may promote rapid populational growth when environmental conditions are favorable. Considering that this analysis is restricted to observations of the 1st and 2nd instars, studies of other developmental stages should be conducted to test this hypothesis.

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SHORT COMMUNICATION

A new species of *Cryptocellus* (Arachnida, Ricinulei) from northwestern Colombia

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Abstract. *Cryptocellus platnicki* sp. nov. is described on the basis of specimens of both sexes from two localities in northwestern Colombia. The new species, which is most similar to *C. glenoides* Cooke & Shadab 1973, brings to 64 the known species of living ricinuleids, and becomes the sixth known from Colombia.

Keywords: Ricinuleids, taxonomy, *Cryptocellus platnicki* sp. nov.

Ricinulei is one of the rarest arachnid orders, comprising 63 living species known to date. Extant representatives are gathered into the family Ricinoididae, which includes the Western African genus *Ricinoides* Ewing 1929, the Central American *Pseudocellus* Platnick 1980, and the primarily South American *Cryptocellus* Westwood 1874. The last genus includes 32 known species (Bonaldo & Pinto-da-Rocha 2003; Harvey 2003; Cokendolpher & Enríquez 2004; Pinto-da-Rocha & Bonaldo 2007; Tourinho & Azevedo 2007; Platnick & García 2008), five of which are present in Colombia: *Cryptocellus magnus* Ewing 1929 (= *C. manni* Ewing 1929), *C. glenoides* Cooke & Shadab 1973, *C. peckorum* Platnick & Shadab 1977, *C. narino* Platnick & Paz 1979 (Ewing 1929; Cooke & Shadab 1973; Platnick & Shadab 1977; Platnick & Paz 1979), and a new species described by Platnick & García (2008).

In the present paper a new species is described from both male and female specimens collected by pitfall traps and tree agitation on recent expeditions to Acandí, department of Chocó, northwestern Colombia (near the border with Panama). The technique of tree agitation consists in shaking a small tree so that specimens in the upper foliage fall on a blanket placed below. With its description, the number of known species of living ricinuleids is raised to 64, six of which are present in Colombia.

METHODS

General terminology follows Platnick & Shadab (1977), except that of male leg III which follows Cokendolpher (2000). Measurements are presented in millimeters and were obtained according to the procedures outlined by Cooke & Shadab (1973), using the program Motic Images 2000 version 1.2 through a PC connected to a Motic Digital Microscope DM-143. Illustrations were prepared with the aid of a *camera lucida* mounted onto a Zeiss Stemi SV 6 stereoscope. The specimens are preserved in 70% ethanol.

Specimens examined in this study are lodged in the following museums: Museo Javeriano de Historia Natural "Lorenzo Uribe S. J.", Pontificia Universidad Javeriana, Bogotá, Colombia (MPUJ) and Museu Nacional, Rio de Janeiro, Brazil (MNRJ).

TAXONOMY

Family Ricinoididae Ewing 1929
Genus *Cryptocellus* Westwood 1874

Cryptocellus Westwood 1874:201.

Type species.—*Cryptocellus foedus* Westwood 1874, by monotypy.

Cryptocellus platnicki sp. nov.
Figs. 1–10

Type material.—*Holotype:* COLOMBIA: *Department of Chocó*: adult male, Acandí, Capurganá, Jardín Botánico del Darién, 08°37′N, 77°21′W, 50 m elev., pitfall, 29 April 2007, E. González, D. Montañez & D. Peña (MPUJ-RIC-002).

Paratypes: COLOMBIA: *Department of Chocó*: 1 adult female, Acandí, Capurganá, Jardín Botánico del Darién, 08°37′N, 77°21′W, 50 m elev., pitfall, 29 April 2007, P. Chávez, L. Leiva & L. Rojas (MPUJ-RIC-003); 1 adult male, Acandí, Capurganá, Vereda Girasoles, 08°37′N, 77°21′W, forest, 330 m elev., ad hoc, 14:00 hours, 8 October 2007, I. Cuadros, A. Rodríguez, L. Restrepo & C. Parra (MPUJ-RIC-004).

Other material: COLOMBIA: *Department of Chocó*: 1 female tritonymph, Acandí, Capurganá, Vereda Girasoles, 08°37′N, 77°21′W, forest, 330 m elev., tree agitation, 15:00 hours, 7 October 2007, F. Niño, S. Arciniegas & G. González (MPUJ-RIC-005); 1 female deutonymph, Acandí, Capurganá, Jardín Botánico del Darién, 08°37′N, 77°21′W, 40 m elev., tree agitation, 08:00 hours, 10 October 2007, C. Latorre (MPUJ-RIC-006).

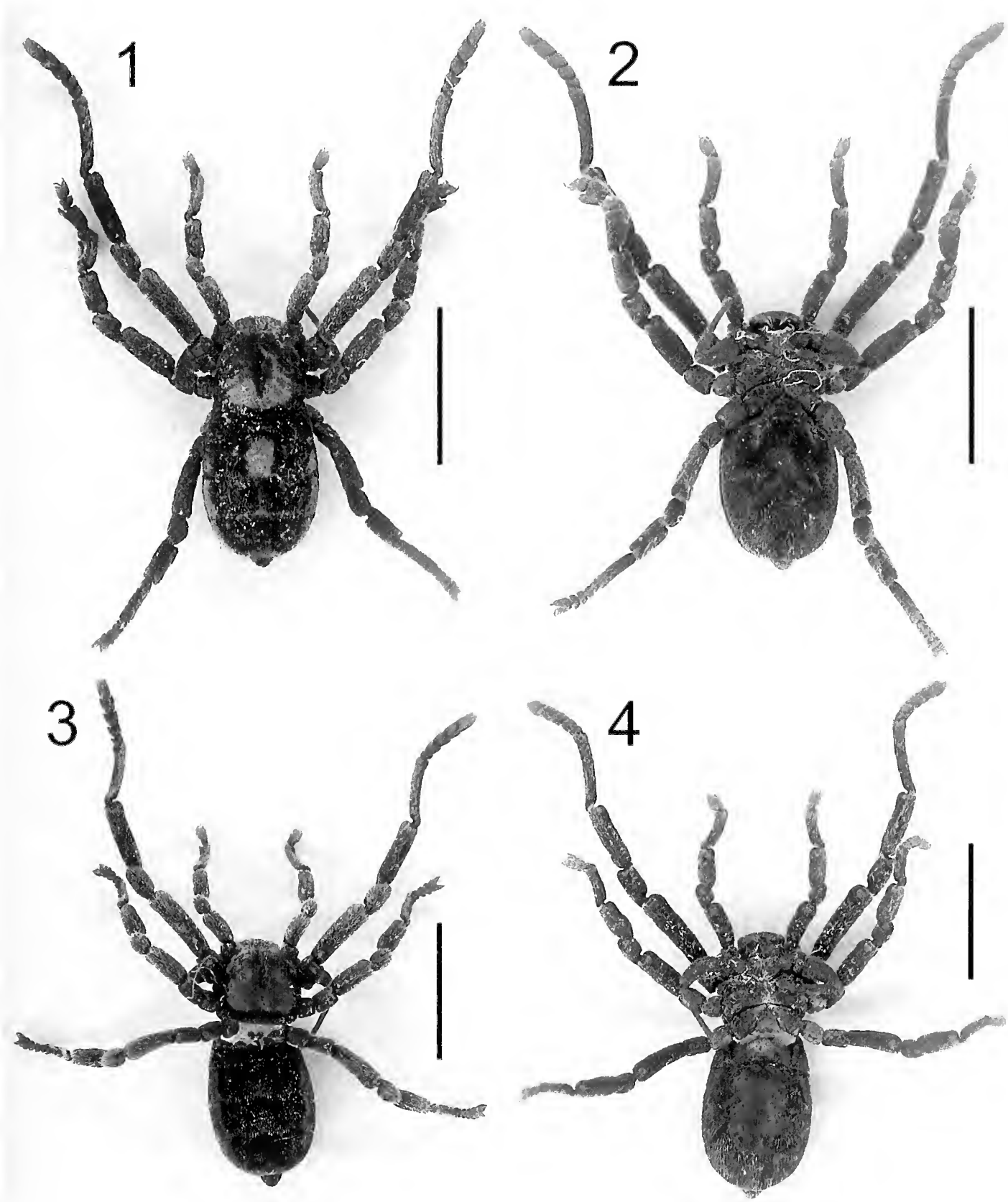
Etymology.—Patronym dedicated to Norman I. Platnick, arachnologist at the Division of Invertebrate Zoology of the American Museum of Natural History, New York, who has published many contributions on the New World ricinuleids.

Diagnosis.—The new species is most similar to *C. glenoides*, with which it shares the following features: (i) carapace, cucullus, abdomen and appendages densely covered with long fine translucent setae; (ii) scale-like setae completely absent; (iii) cucullus with only some scarce tubercles restricted to anterior and lateral margins; (iv) earapace without pits (Fig. 5); (v) trochanter IV unmodified; (vi) basal segment of pygidium unnotched on either dorsal or ventral posterior borders; (vii) fixed process of the male copulatory apparatus with an anteroventral ledge. The new species can be readily distinguished from *C. glenoides* by the following: (i) shape of the carapace, which is subtriangular in the new species (Fig. 5), but almost quadrangular in *C. glenoides*; (ii) shape of the movable process of the male copulatory apparatus, which is curved and not bifid in the new species (Fig. 7), but almost straight, dorsoventrally flattened, and bilobated in *C. glenoides* (Cooke & Shadab 1973:figs. 27, 37); (iii) shape of the female spermathecae: see Figures 9, 10 for the new species, and Platnick & Shadab (1976:fig. 17) for *C. glenoides*.

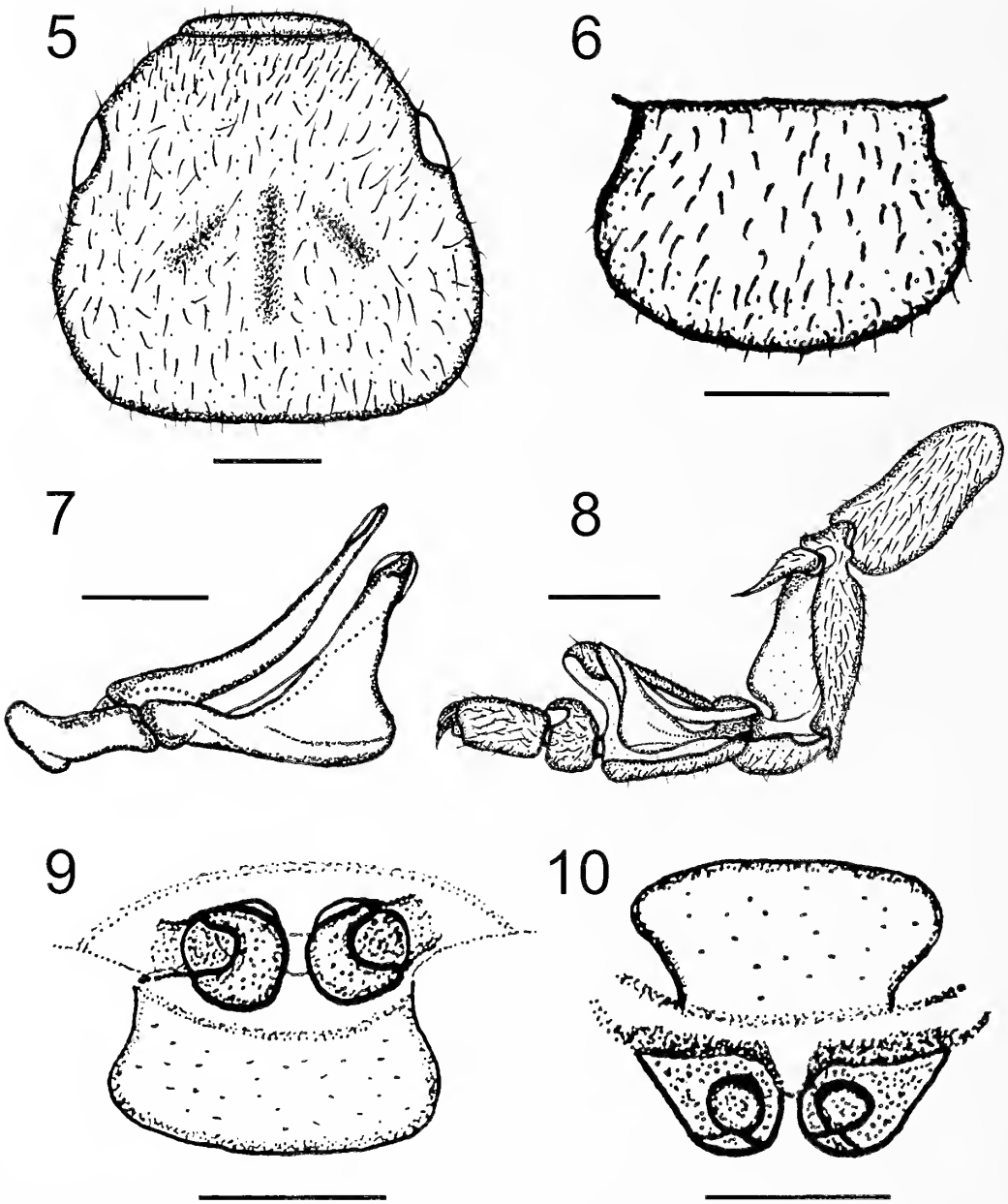
Description based on male holotype (MPUJ-RIC-002).—*Coloration:* Body and appendages reddish-brown, except pedipalps, chelicerae, and distal segments of legs, which are yellowish to light-red; abdominal articular membranes yellow.

Setation: Carapace, cucullus, abdomen and legs densely covered with long fine translucent setae uniformly distributed throughout (Figs. 5, 6, 8); sternal region and pedipalps with shorter hairs.

Carapace: Subtriangular; as long as wide, widest at middle of leg III; with smooth, pale translucent areas located at margins between



Figures 1–4.—*Cryptocellus platnicki* sp. nov.: 1, 2. Male holotype (MPUJ-RIC-002), dorsal and ventral views; 3, 4. Female paratype (MPUJ-RIC-003), dorsal and ventral views (the abdomen was separated to study the spermathecae). Scale bars: 3 mm.



Figures 5–10.—*Cryptocellus platnicki* sp. nov. 5–8. Male holotype (MPUJ-RIC-002): 5. Dorsal view of the carapace; 6. Cucullus; 7. Anterior view of movable (above) and fixed (below) processes of the copulatory apparatus. 8. Anterior view of leg III. 9, 10. Female paratype (MPUJ-RIC-003): 9. Spermathecae, anterior view; 10. Spermathecae, posterior view. Scale bars: 0.5 mm (Figs. 5, 6, 8); 0.25 mm (Figs 7, 9, 10).

legs I and II; with very few tubercles and devoid of pits; median longitudinal furrow present, beginning at level of junction between coxae I and II, ending near posterior end of carapace (Fig. 5).

Cucullus: Slightly wider than long, widest anteriorly (Fig. 6); with few tubercles restricted to anterior and lateral margins.

Chelicerae: Movable fingers armed with nine teeth almost equally sized (both chelicerae); fixed finger of left chelicera with five teeth increasing in size distally; fixed finger of right chelicera also with five teeth, but third most distal tooth considerably enlarged (equal to fourth on left finger), and fourth most distal tooth markedly reduced.

Sternal region: Coxae I not meeting tritosternum, coxae II meeting posteriorly, coxae III meeting at midline, coxae IV meeting anteriorly.

Abdomen: Longer than wide, widest at anterior margin of tergite XII; almost devoid of tubercles, except for few placed close to midline on median plates of tergites XI–XII; median plates of tergites XI–XIII and corresponding sternites with paired lateral depressions between which median elevation occurs on dorsal plates; all median plates wider than long. Basal segment of pygidium unnotched on either dorsal or ventral posterior borders.

Pedipalps: With few tubercles on trochanters, and others more abundant on femur basally; femora considerably enlarged; both claws with numerous minute teeth.

Legs: With tubercles somewhat dispersed on all segments; trochanter IV unmodified; tarsal claws short, strongly curved. Copulatory apparatus as in Figures 7, 8, with movable process curved and not bifid, and fixed process with an anteroventral ledge.

Comparison with the female paratype (MPUJ-RIC-003).—Coloration as in male. Left chelicera with ten teeth on movable finger. Abdomen with shorter setae throughout, denser tuberculation on tergite XII. Spermathecae as in Figures 9, 10. Pedipalp femur with fewer basal tubercles.

Measurements (mm).—*Male holotype (MPUJ-RIC-002):* Body total length, excluding pygidium 4.71; cucullus 0.78 long, greatest width 0.96; carapace 1.56 long, 1.61 wide between legs II–III; abdomen 2.37 long (excluding pygidium), 2.05 wide near middle of tergite XII where widest; pedipalp femur 0.76 long, greatest diameter 0.38; pedipalp tibia 1.0 long, greatest diameter 0.19; femur I 0.81 long, 0.38 in diameter; femur II 2.0 long, 0.40 in diameter.

Male paratype (MPUJ-RIC-004): Body total length, excluding pygidium 5.14; cucullus 0.84 long, greatest width 0.94; earapace 1.71 long, 1.72 wide between legs II–III; abdomen 2.59 long (excluding pygidium), 2.09 wide near middle of tergite XII where widest; pedipalp femur 0.79 long, greatest diameter 0.44; pedipalp tibia 1.13 long, greatest diameter 0.21; femur I 0.83 long, 0.40 in diameter; femur II 1.73 long, 0.45 in diameter.

Female paratype (MPUJ-RIC-003): Body total length, excluding pygidium 5.08; cucullus 0.90 long, greatest width 1.01; carapace 1.58 long, 1.96 wide between legs II–III; abdomen 2.60 long (excluding pygidium), 2.21 wide near middle of tergite XII where widest; pedipalp femur 0.89 long, greatest diameter 0.48; pedipalp tibia 1.18 long, greatest diameter 0.20; femur I 0.86 long, 0.39 in diameter; femur II 1.61 long, 0.47 in diameter.

Variation.—The male paratype (MPUJ-RIC-004) bears 4:3 teeth on the fixed fingers of chelicerae, and 8:8 on the movable fingers. *Nymphs:* the coloration is yellowish; the carapace, cucullus, sternal region, tergites and sternites are densely covered with tubercles similar to those of the legs. This indicates that the granulation varies among different stages.

Distribution.—*Cryptocellus platnicki* is known from two localities: Jardín Botánico del Darién and Vereda Girasoles, Capurganá, Acandí, department of Chocó. These localities belong to the Colombian Chocó-Magdalena Biogeographic Region as defined by Hernández-Camacho et al. (1992), an area of confluence of both Central and South American elements of fauna characterized by a high level of endemism.

Remarks.—As noted already, *C. platnicki* is most similar to *C. glenoides*, which was placed as the most plesiomorphic branch of the *C. magnus* species group by Platnick & Paz (1979:fig. 1) due to its straight and massive movable process of the male copulatory apparatus characteristic of this group. In a later contribution, however, Platnick & Shadab (1981) argued that *C. glenoides* is probably a member of the *C. centralis* Fage 1921 species group due to the presence on this species of an anteroventral ledge on the fixed process of the male copulatory apparatus on whose basis the *C. centralis* group is defined (Platnick & Shadab 1981) and suggested that the straight and massive movable process may have evolved in parallel in this species. The presence in *C. platnicki* of the anteroventral ledge on the fixed process and the curved movable process may indicate that the new species could belong to the *C. centralis* group, probably representing the sister speeies of *C. glenoides* supported on their common branch by the massive movable process; however, further synapomorphies are needed to test the monophyly of either the *C. magnus* or the *C. centralis* groups and, as noted by Platnick & Shadab (1981) for *C. glenoides*, resolve this character contradiction.

Other material examined.—*Cryptocellus glenoides:* COLOMBIA: *Department of Valle del Cauca*: 1 adult ♂, Dagua, El Salto, 03°39′N, 76°41′W, 30 August 2006, A.P.L. Giupponi (MNRJ). *Cryptocellus peckorum:* COLOMBIA: *Department of Amazonas*: 1 adult ♀, Leticia, indigenous community Monilla Amena, Varzea, 04°06′ S, 69°55′W, 70 m elev., pitfall, 6 September 2005, G. Rodríguez (MPUJ-RIC-001).

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The authors are grateful to Norman I. Platnick (American Museum of Natural History, New York), Paula E. Cushing (Denver Museum of Nature & Science, Denver), Mark S. Harvey (Western Australian Museum, Perth), and an anonymous reviewer for reading an earlier draft of the manuscript and making valuable comments that led to its improvement. To N.I. Platnick for his assistance with some laboratory procedures, and to Louis Sorkin (AMNH), Ricardo Pinto da Rocha (Universidade do São Paulo, Brazil), and Piotr Naskrecki (Harvard University, Cambridge) for their kind help in acquiring relevant literature. Additional thanks are due to all the members of the Museu Nacional (Rio de Janeiro) for their collaboration and hospitality during the first author's visit to the MNRJ in August 2007. Thanks also go to Giovanny Fagua (Pontificia Universidad Javeriana, Bogotá) for the loan of some laboratory equipment, and to the students of the course "Zoología de Invertebrados - 2007" at the PUJ for their work and effort in the field. Thanks also to Luis G. Pérez (PUJ) for his help in obtaining the measurements, and to Miguel León and Nestor García (PUJ) for the loan of the *camera lucida*. Finally, thanks to Ricardo Pinto da Rocha and the organizing committee of the 17th International Congress of Arachnology for financial support that allowed the first author to attend the ISA Congress.

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SHORT COMMUNICATION

On the genus *Neostothis* Vellard (Araneae, Nemesiidae)

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Abstract. To date, the genus *Neostothis* Vellard is known only from its type species *Neostothis gigas* Vellard 1925, described on the basis of a single male and some females from Reserva Biológica do Alto da Serra de Paranapiacaba, Santo André, São Paulo, Brazil. The type specimens, which should be deposited in the collection of the Instituto Butantan are lost. Specimens matching the description of *N. gigas*, collected in the type locality, allowed us to designate a neotype and provide more information on the genus and species.

Resumo. Até a presente data, o gênero *Neostothis* Vellard é conhecido somente pela espécie tipo *Neostothis gigas* Vellard 1925, descrita com base em um macho e algumas fêmeas da Reserva Biológica do Alto da Serra de Paranapiacaba, Santo André, São Paulo, Brasil. Os exemplares-tipo, que deveriam estar depositados na coleção do Instituto Butantan, estão perdidos. Exemplares machos e fêmeas de *N. gigas*, coletados na localidade-tipo, permitiram estabelecer um neótipo e melhorar o conhecimento do gênero e da espécie.

Keywords: Atlantic Forest, Mygalomorphae, *Neostothis gigas*, Pycnothelinae

The family Nemesiidae was proposed in 1985 by Raven by elevating Simon's Nemesiae Simon 1892, synonymizing Pycnothelidae with it, and transferring to it some genera previously placed in Ctenizidae (Raven 1985). To date, the family includes six subfamilies, 41 genera, and 340 species distributed worldwide (Platnick 2008).

Two subfamilies include genera with species known to occur in Brazil: Pycnothelinae, with *Chaco* Tullgren, *Hermachura* Mello-Leitão, *Neostothis* Vellard, *Prorachias* Mello-Leitão, *Psalistopoides* Mello-Leitão, *Pselligmus* Simon, *Pycnothele* Chamberlin, *Rachias* Simon and *Stenoterommata* Holmberg; and Anaminae, with *Acanthogonatus* Karsch, *Longistylus* Indicatti & Lucas and *Hermacha* Simon (Raven 1985; Platnick 2008).

The monotypic genus *Neostothis* was proposed by Vellard (1925), to include the type species, *N. gigas*, described based on a male and females from Reserva Biológica do Alto da Serra de Paranapiacaba, Santo André, São Paulo, Brazil. Vellard originally placed the genus in Barychelidae, probably due to the wide labium with few cuspules, absence of tibial apophysis, short apical segment of the posterior lateral spinnerets and well developed leg scopulae, mainly on tarsi I and II, resembling claw tufts. Raven (1985), based on Vellard's description, considered *Neostothis* a junior synonym of *Chaco* Tullgren, and transferred the genus from Barychelidae to Nemesiidae (Pycnothelinae), due to the presence of scopula on tarsi III and IV, wide labium, and absence of third claw. Goloboff (1995) reestablished *Neostothis* based on characters previously mentioned by Vellard: lack of keels on the male palpal bulb and absence of tibial apophysis.

During field work in the type locality, several male and female specimens of *N. gigas* were collected. These specimens yield a better knowledge about the genus and species and enabled the establishment of a neotype.

METHODS

The material examined is deposited in the following institutions (abbreviation and curator in parenthesis): Instituto Butantan, São Paulo (IBSP, A.D. Brescovit), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto da Rocha) and American Museum of Natural History, New York (AMNH, N.I. Platnick). Spine notation follows Petrunkevitch (1925). All measurements are in millimeters and were taken with an ocular lens. The length of leg segments was measured between joints in dorsal view. Length and width of carapace, eye tubercle, labium and sternum are maximum values obtained. The total body length excludes chelicerae, pedicel and spinnerets. All drawings were made with a drawing tube (Leica MZ 12.5). Spermathecae were cleared with clove oil and illustrated in ventral and dorsal view. Abbreviations: AME, anterior median eyes; ALE, anterior lateral eyes; PME, posterior median eyes; PLE, posterior lateral eyes; PLS, posterior lateral spinnerets; d, dorsal; v, ventral; p, prolateral; r, retrolateral; ap, apical.

TAXONOMY

Neostothis Vellard 1925

Neostothis Vellard 1925:79, 82, pl.15. Type species by monotypy, *Neostothis gigas* Vellard 1925. Raven 1985:103; Goloboff 1995:168; Platnick 2008.

Diagnosis.—Males of *Neostothis* (Figs. 2 a–c) resemble those of *Prorachias* Mello-Leitão by the absence of keels on the embolus (Lucas et al. 2005, figs. 1–3), but can be distinguished by the weak rastellum; intercheliceral tumescence large, pale yellow and covered with many modified setae; shape of the palpal tibia (Figs. 2 a, c); and absence of a third claw on all tarsi. Females resemble those of *Pycnothele* Chamberlin by the presence of a supraspermathecal chamber (Goloboff 1995, fig. 115 g, h) (Figs. 2 e, f). They differ by the chamber less sclerotized on lateral sides and located more centrally (Figs. 2 e, f), by the spermathecal lobe three or four times larger than in *Pycnothele*, and by the scopula of tarsi III entire.

Description.—See species description.

Distribution.—Known only from the state of São Paulo, southeastern Brazil.

Neostothis gigas Vellard 1925
(Figs. 1 a–d, 2 a–f)

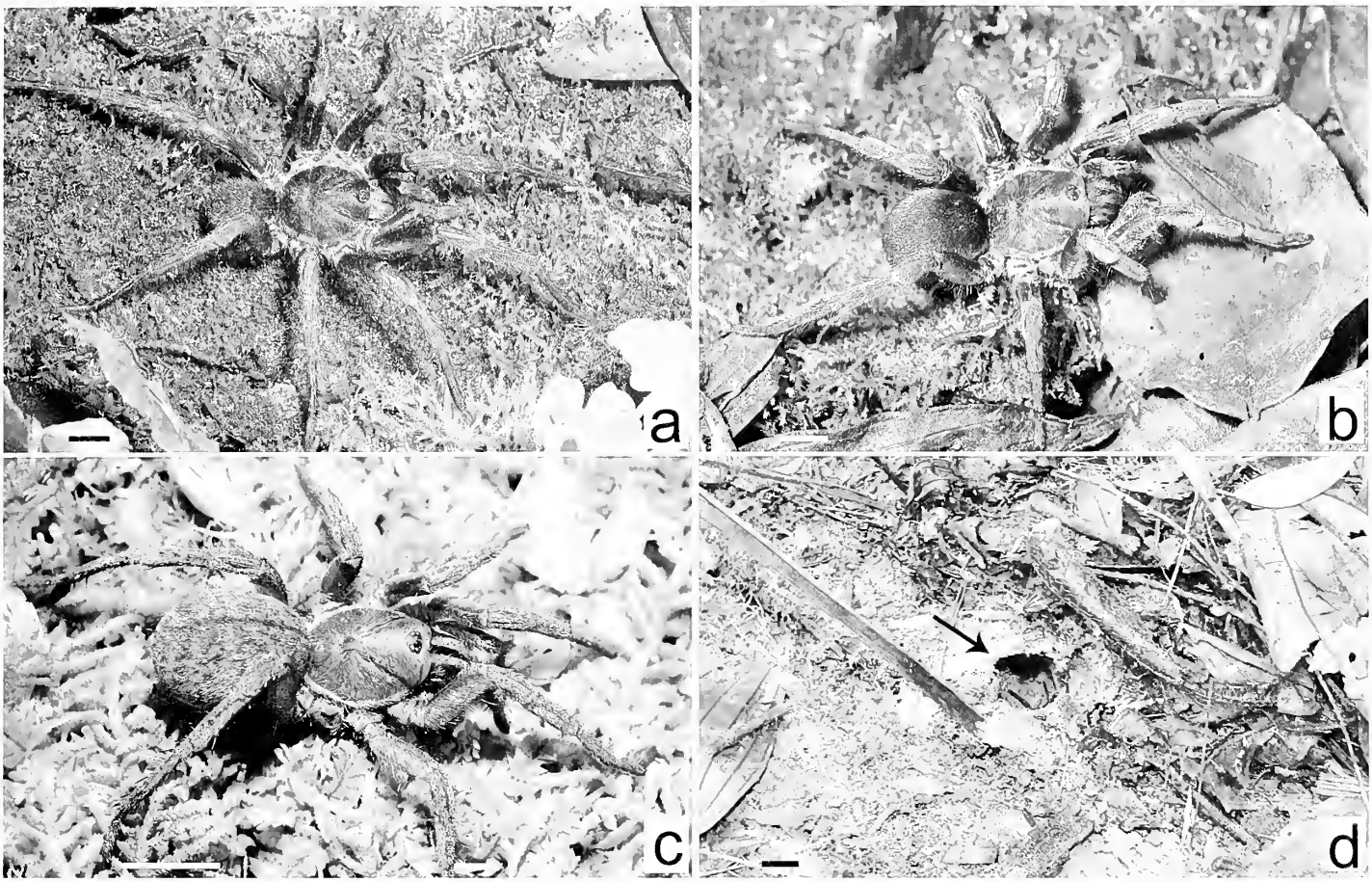

Figure 1.—*Neostothis gigas*. a–c. Body, dorsal view: a. Male; b. Female; c. Juvenile; d. Burrow, frontal view. Scale bars: a–c = 5 mm; d = 20 mm. Photos: a–c. F.U. Yamamoto; d. R.P. Indicatti.

Neostothis gigas Vellard 1925:79, 82, pl. 15 (male holotype from Reserva Biológica do Alto da Serra de Paranapiacaba (23°46′00″–23°47′10″S; 46°18′20″–46°20′40″W), Santo André, São Paulo, Brazil, deposited in IBSP 104, lost, neotype here designated IBSP 13509); Raven 1985:103; Goloboff 1995:168; Platnick 2008.

Other material examined.—BRAZIL: *São Paulo:* Santo André (Reserva Biológica do Alto da Serra de Paranapiacaba [23°46′00″–23°47′10″S; 46°18′20″–46°20′40″W]), 24 males, 18–19.XII.2006, M. Uehara-Prado leg. (IBSP 13493–13495; 13497; 13498–13500; 13506; 13508; 13510; 13512; 13513; 13517; 13518); 5 males, 11–12.I.2007 (IBSP 13509; 13516; 13501; 13504; 13505;13521); 2 males, 12.I.2006 (IBSP 13496; 13502); 8 males and 3 females, 16–17.XI.2006 (IBSP 13519; 13515; 13503; 13511; 13514; 13507; 145499; 14500); 1 female, 17.VIII.1997, I. Grantsau leg. (IBSP 8290); 1 female, 17.III.1998, C. Albuquerque leg. (IBSP 10590); 2 females, 13.XII.2003, R.P. Indicatti leg. (IBSP 13229, 14371); Ribeirão Pires [23°43′S; 46°25′W], 1 male, 27.IX.2004, O.R. Silva leg. (AMNH); São Lourenço da Serra [23°52′S; 46°57′W], 1 female, 16.XII.2003, R.P. Camargo leg. (IBSP 10382); 1 male, X.2005, R. Krett de Oliveira leg. (IBSP 12266); Ubatuba (Parque Estadual Ilha Anchieta [23°32′S; 45°03′W]), 1 female, 23-30.VII.2001, C.A. Rheims, D.F. Candiani, C.A.R. Souza and A.G. Suguimoto leg. (IBSP 12371); São Sebastião [23°48′S; 45°25′W] (Barra do Una), 1 male, 29.I.1997, B.A. Mattos-Netto leg. (IBSP 8214); 1 male (IBSP 14364); (Barra do Sahy), 1 male, 21.II.1994, V. Durion leg. (IBSP 8213); 1 male, 31.I.2006, E.F. Santos leg. (IBSP 8216); 1 male, I.1986, E. Cibelle leg. (IBSP 4585); (Juqueí), 1 male, XI.1976, G. Peixoto leg. (IBSP 14363); 1 male, I.2007 (IBSP 13660); Mogi das Cruzes [23°31′S; 46°10′W], 3 males, 21–23.IX.2004, A.E.G. Monteiro leg. (MZSP 27653; 27654); (Parque das Neblinas), 4 males and 2 females, 03.I.2006, M. Uehara-Prado leg. (IBSP 13264; 13262; 13261; 13263); 1 female, 20.III.2006 (IBSP 13265); Salesópolis (Estação Biológica de Boracéia [23°32′S; 45°51′W]), 5 males and 1 female, 08–10.XII.2005, M. Uehara-Prado leg. (IBSP 13271; 13272; 13273; 13274; 13275; 13266); 1 female, 13–17.III.2007, F.U. Yamamoto leg. (IBSP 13458); 01–08.XI.2006, R. Recoder leg. (IBSP 14291; 14292; 14293); 2 males, 08.IV.2005 (IBSP 13268); 2 males, 09–10.IX.2005 (IBSP 13269; 13270); 2 females, (22160); VI.2003, J.P.L. Guadanucci leg. (MZSP 27673); Juquitiba [23°55′S; 47°4′W], 1 female, IX.1979, O. Martinez leg. (IBSP 4479); 1 female, XI.1979, P.G. Butazzi (AMNH); (Juquiazinho), 1 male (IBSP 14501); Ilha Bela (Parque Estadual de Ilha Bela [23°8′–23°50′S; 45°18′–45°22′W]), 3 males and 5 females, 16.I.1998 (IBSP 13103; 13104; 13105; 13106; 13107; 13108; 13109; 13110); Itanhaém [24°10′S; 46°46′W], 1 male, V.1985, R. Pinheiro leg. (IBSP 4585); São Paulo [23°31′S; 46°37′W], 1 male, 13.XI.1991, R.C. Rossger leg. (IBSP 14290); (Parque Estadual do Jaraguá), 1 male, 23.X.2001, R.P. Indicatti leg. (IBSP 3825); 1 male, 13.X.1997, M. Tokura leg. (IBSP 8217); (Guarapiranga), 1 male, 24.XI.2003, V.R. Santos leg. (IBSP 10626); (Parelheiros), 1 male, XII.1975, R. Schwarck leg. (IBSP 4173); (Parque Estadual da Serra do Mar, Núcleo Curucutu [23°59′S; 46°44′W]), 1 male, 24.V.2006, M. Forlan leg. (IBSP 13883); Vargem Grande do Sul [21°49′S; 46°52′W], 1 female, 10.X.1980, T. Siola leg. (IBSP 4569).

Diagnosis.—See genus diagnosis.

Description.—*Male* (neotype IBSP 13509). Coloration pattern: carapace, abdomen and legs dark brown (Fig. 1 a). Total length 22.0, Carapace 10.75 long, 12.5 wide, fovea short and procurved. Clypeus narrow 0.87. Anterior eye row procurved, posterior slightly recurved. AME 0.41, ALE 0.47, PME 0.25 and PLE 0.46. Overall shape of eye

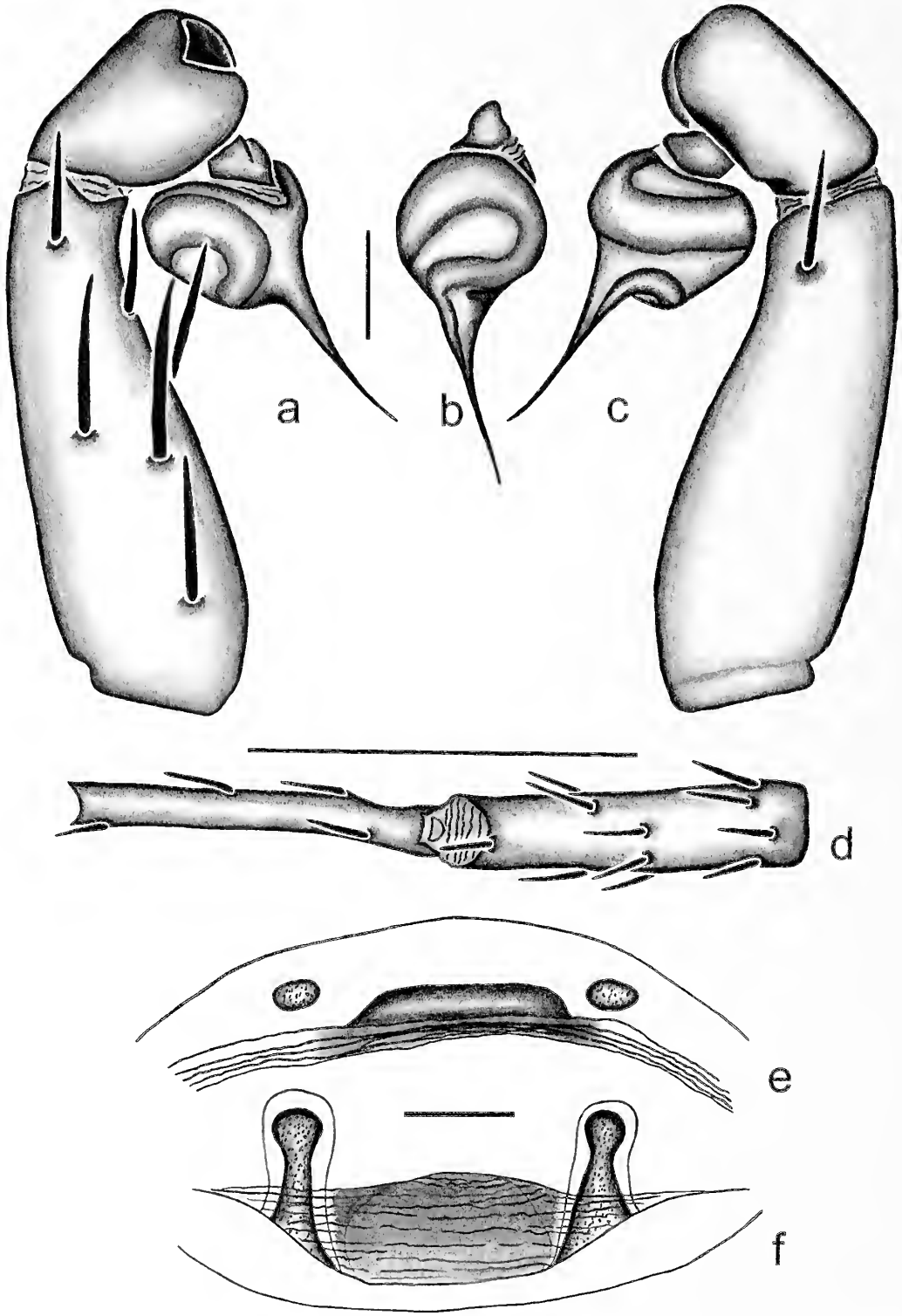

Figure 2.—*Neostothis gigas*. a–c. Left palpal bulb: a. Prolateral view; b. Ventral view; c. Retrolateral view. d. Male, left leg, tibia and metatarsi I, ventral view. e, f. Female supraspermathecal chamber: e. Frontal view; f. Dorsal view. Scale bars = 1 mm.

group trapezoidal, wider than long. Basal segment of chelicerae with 10–11 promargin teeth in a row and rastellum with very strong setae. Intercheliceral tumescence pale yellow, large, covered with many dark modified setae. Labium 1.75 long, 1.0 wide, with three cuspules. Each endite with 30 cuspules. Serrula present. Sternum oval 4.75 long, 5.62 wide. Six sternal sigilla, posterior submarginal three times size of anterior. Leg measurements: **I:** femur 11.0/ patella 6.25/ tibia 8.75/ metatarsus 9.75/ tarsus 5.25/ total 41.0; **II:** 10.62/ 5.75/ 8.37/ 9.62/ 5.5/ 39.86; **III:** 10.0/ 5.0/ 7.25/ 11.25/ 5.37/ 38.87; **IV:** 12.25/ 5.62/ 9.75/ 14.5/ 5.25/ 47.37; spination: **palp:** femur d0-0-0-0-0-2-0, patella p0-1-1-0-1-0, tibia v0-0-1p-0, p0-1-0-2-0-1-1, r0-0-0-0-0-1; **legs: I:** femur d0-1-1r-1-2-1-2-1-2-0, patella p0-0-1-0-1-0, tibia v1p-2r-0-1-2r-1p (ap), p2-0-1-1-1-0-0, megaspine absent, metatarsus v0-1p-1r-0-1r-0-0-0, p1-0-0-1-0-0-1, r0-0-1-0; **II:** femur d0-1-2-1-2-1-2-1-2, patella v0-1r-0, p0-0-1-1-0, tibia v1p-2r-0-0-1p-1-1r-0-0-3ap, p1-1-0-1-0-1-1-0-0, metatarsus d0-0-0-1-0-0, v0-1p-1r-0-0-1r-1p-0-0-2ap, p1-0-0-1-0-0-0-1, r0-0-0-0-1-

0-0-1; **III:** femur d0-1-2-1-2-1-2-1-2, patella p0-1-1-1-0, r0-1-0-0, tibia d0-1-1-0-0-0-1-0-0, v2r-2p-0-0-1p-1r-0-0-3ap, p1-1-1-0, r1-0-1-0-1-0, metatarsus d2r-1p-1-1r-1p-1r-1p-0-2, v0-1p-1r-0-0-1p-1r-1p-0-3ap, p0-1-0-1-0-1-0-1, r1-0-1-0-1-1-0-0; **IV:** femur d0-1-1-2-1-2-1-2, patella p0-1-1-1-0, r0-1-0-0, tibia d0-1r-1-0-0-0-1-0, v1r-1p-0-0-1p-1p-1r-0-0-3ap, p1-0-1-0-1-0, r1-0-1-0-1-0-1-0-1, metatarsus d0-2r-2-1p-1r-0-1p-1r-0-2, v1r-1-1p-0-1p-1p-1r-0-3ap, p0-1-0-0-1-0-1-0, r0-0-1-0-0-1-0-1-0. Metatarsi I with a slight retrolateral basal curvature (Fig. 2 d). Tarsi I–IV flexible. Scopulae divided on tarsi I–V (more dense and projected anteriorly on tarsi I–II, resembling claw tufts) and on anterior fourth of metatarsi I–II. Superior tarsal claws large with two rows of 5–8 teeth on tarsi I; 5–9 on tarsi II, 5–10 on tarsi III and 5–11 on tarsi IV. Third claw absent on all tarsi. Four spinnerets, PLS three segmented, basal segment 1.25, median segment 0.75, apical segment, domed 0.37 long. Palpal tibia short and basally dilated. Bulb piriform with long and slender embolus, slightly curved dorsally (Figs. 2 a–c).

Female. (IBSP 8290). Coloration pattern as in male (Fig. 1 b). Total length 24.37. Carapace 13.12 long, 11.25 wide, fovea short and procurved. Clypeus narrow 1.25. Anterior eye row procurved, posterior slightly recurved. AME 0.42, ALE 0.47, PME 0.25, PLE 0.45. Overall shape of eye group trapezoidal, wider than long. Basal segment of chelicerae with 11 promargin teeth in a row and rastellum with very strong setae. Intercheliceral tumescence absent. Labium 1.37 long, 2.12 wide, with four cuspules. Each endite with 28 cuspules. Serrula absent. Sternum oval 6.62 long, 5.87 wide. Six sternal sigilla, posterior and median submarginal, posterior three times size of anterior. Leg measurements: **I:** femur 10.0/ patella 6.25/ tibia 6.62/ metatarsus 6.5/ tarsus 3.62/ total 32.99; **II:** 9.37/ 5.62/ 6.0/ 6.25/ 3.75/ 30.99; **III:** 8.37/ 5.0/ 5.25/ 7.25/ 3.5/ 29.37; **IV:** 11.25/ 5.5/ 7.5/ 12.12/ 3.75/ 40.12; spination: **palp:** femur d0-0-0-0-1p , tibia v2-0-2-0-4ap, p0-0-1-0, tarsus v1r-0-0-0-0; **legs: I:** femur d0-0-0-0-0-1p-0, tibia v0-1-0-0-1p-1-0-0-1p (ap), p0-0-1-0, metatarsus v1p-1r-0-0-1r-0-0-0-0; **II:** femur d0-0-0-0-0-1p-0, patella d0-0-0-1p-0, tibia v1p-1r-0-0-2-1r-0-0-3ap, p0-1-0-1-0, metatarsus v0-1p-1r-0-0-1r-0-0-2ap, p0-0-1-0-0-0; **III:** femur d0-0-0-0-1r-0, patella p0-0-1-1-1-0, tibia v0-1r-1p-0-0-2-0-0-0-2ap, p0-1-0-1-0, r0-1-0-0, metatarsus d0-0-2-0-0-0-2-0, v0-0-1p-2r-1p-0-0-1r-1p-3ap, p0-0-1-0-0-0-1-1-0, r0-0-1-0-0-1-0-0-2-0-0-3ap; **IV:** patella p0-0-1-1-1-0, tibia v1r-1p-0-0, r0-1-0-1-0, metatarsus d0-0-0-1r-1p1-0-0, v0-1p-1r-0-1p-2-0-2-0-1r-1p-0-3ap, p0-1-0-0-1-0-0-1-1-1-0, r0-1-0-1-0-1. Tarsi I–IV flexible. Scopulae present on tarsi I-IV and on metatarsi I–II. Scopulae on tarsi and metatarsi I–II more dense and projected on lateral sides. Scopulae on tarsi I–II projected anteriorly (resembling claw tufts). Scopulae on tarsi I–II and metatarsi I symmetric and metatarsi II asymmetric. Scopula of tarsi IV dividided by one band of 4-8 setae. Superior tarsal claws large with two rows of 5–6 teeth on tarsi I, 5–6 on tarsi II, 5–7 on tarsi III and 6–9 on tarsi IV. Third claw absent on all tarsi. Four spinnerets, PLS three segmented, basal segment 1.87, median segment 0.87, apical segment domed 0.62 long. Spermathecae formed by two receptacles with a wide base and dilated apical region (Figs. 2 e, f).

Note.—Coloration pattern in juvenile: carapace brown with golden setae on lateral sides and legs brown with golden-yellow setae and dark brown mottles. Abdomen dorsally and ventrally brown with random symmetric pale mottles in life (Fig. 1 c).

Variation.—Males (n = 20): total length 19.6–24.7; carapace 10.6–13.7; endites with 25–58 cuspules. Females (n = 10): total length 22.7–28.4; carapace 10.1–13.3; endites with 40–68 cuspules. Posterior and median sternal sigilla can be marginal.

Natural history.—This species occurs in Atlantic Forest areas, 0-900 m elev., mainly in the littoral of the state of São Paulo. Adult specimens can be found in burrows of simple vertical or horizontal tunnels with 2.0–3.5 cm diameter and 10–20 cm length in ravines, from as low as ground level to as high as 1 m. The inside of the burrow is covered by a thin layer of silk. The opening is protected during the day by a thin layer of silk, which the spider breaks through in the beginning of the night, when it ambushes its prey. In captivity, they usually close the burrow opening with a layer of silk and earth.

Distribution.—Known only from the state of São Paulo, southeastern Brazil.

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SHORT COMMUNICATION

Notes on the life history traits of *Rhopalurus rochai* (Scorpiones, Buthidae) under different feeding regimes

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Abstract. *Rhopalurus rochai* (Borelli 1910) is a very common scorpion species found in the semiarid areas of Pernambuco State, Brazil. This work describes the life history traits of 1st instar *R. rochai* such as litter size, development time, dispersal, and survivorship. The development of 2nd instar juveniles under different feeding regimens was also investigated to determine the effect of food and body mass on intermolt period and number of ecdyses. Field-collected females displaying an enlarged mesosoma were observed daily in the laboratory to obtain newborns that were used to assess events in the 1st instar. Females gave birth on average to 35.8 young (range = 23–55). The duration of the 1st instar (from eclosion to ecdysis) ranged from 7 to 10 days (n = 179). Dispersal started as early as one day following ecdysis and lasted up to 9 days post-molt. All starved juveniles died between days 11 and 30 of the 2nd instar. Increasing food ingestion did not enhance the probability of molting, but decreased risk of mortality and increased the time to the second molt. The relationship between the weight changes during feeding experiments suggests that the threshold weight for molt is 34.3 mg. Together these results suggest that developmental periods for *R. rochai* are slightly greater than those recorded for other buthid genera. These results indicate that there may be inherent physiological costs associated with rapidly increasing mass that may strongly impact foraging strategy.

Keywords: Development time, dispersal time, scorpion, starvation, molt

The genus *Rhopalurus* (Thorell 1876) belongs to the family Buthidae which, along with Liochelidae, Euscorpiidae, Chactidae, and Bothriuridae, forms the Brazilian scorpiofauna (Soleglad & Fet 2003). Nine species of this genus (Lenarducci et al. 2005) are known in Brazil and occur in the Central and Northeast regions within the *cerrado* (Brazilian savannas) and *caatinga* (Lourenço 1986). Despite numerous studies on the taxonomy and biogeography of *Rhopalurus* (Mello-Leitão 1945; Lourenço 1986; Lourenço & Pinto-da-Rocha 1997; Manzanilla & De Sousa 2003; Lenarducci et al. 2005), there is little information on its reproduction, postembryonic development, and nutrition.

The reproductive fitness of females and individual life span are important factors in establishing the population size of a species. The number of offspring produced by a female is one measure of reproductive fitness, and there may be a positive or negative correlation between litter size and female body mass (Lourenço et al. 1996). The duration of postembryonic development is a key factor in determining generation time, with shorter durations lowering the risk of mortality before reaching reproductive maturity and enhancing individual fitness. On the one hand, this type of growth is frequently associated with higher feeding and food assimilation rates in conjunction with a more efficient conversion of food into biomass (Danner & Joern 2003; Branson 2004; McPeek 2004; Stoks et al. 2005). On the other hand, longer development cycles are generally associated with low mass-accumulation rates and higher reproductive costs, such as delayed sexual maturation (Stearns & Koella 1986; Higgins & Rankin 1996; Higgins 2000) and a higher risk of mortality before reaching adulthood (Higgins & Rankin 1996).

Food availability in the field is influenced by seasonal variation, and food shortage is a constraint that terrestrial invertebrates often have to contend with. Such a shortage is likely to affect survival (Iida & Fujisaki 2007) and reproductive output (Bauerfeind & Fischer 2005), particularly in arthropods with long life cycles. Being animals with an extended life span, range = 6–83 months (Polis & Sissom 1990), scorpions will suffer the impact of environmental variation in food availability. These animals are widely distributed throughout the world, but nutritional bases for scorpion growth and development are usually under-investigated. Even the baseline data on their nutritional needs for survival or molting are lacking.

We describe in this paper some observations about the litter size, dispersal time, and 1st instar duration and survival of *R. rochai* and compare this information to available data on other genera of Buthidae. Considering that nutrition is an important aspect in determining growth and development in an organism, the effects of body mass and molting for individuals during 2nd instar development are also presented.

METHODS

Females of *R. rochai* (n = 5) were collected in Limoeiro municipality in the Agreste Mesoregion and Medio Capibaribe Microregion of Pernambuco State, Brazil (area = 277.54 km^2; 07°52′29″ S, 35°27′01″ W; 138 m elev.), 90.9 km from the state capital, Recife. The climate is wet tropical with dry summers. The rainy season starts in January/February and ends in September, but may last until October. The specimens were collected under accumulations of rocks from soil preparation for corn and bean cultivation or from pastures at sites with rock outcrops and low-height deciduous and semi-deciduous plants typical of the agreste (Beltrão et al. 2005). Pregnant females (displaying a dilated mesosoma) were kept in individual plastic containers (8.5 cm diameter × 7.8 cm high) with an assay tube containing cotton soaked in water and a cardboard piece for shelter. They were fed adult *Periplaneta americana* (Linnaeus 1758) once every 15 days. In the laboratory, the temperature was maintained at environmental conditions of 28° ± 3° C with 12L:12D photoperiod. Observations were made daily to record the period in which the young were born

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Table 1.—Litter size, first instar duration, survivorship and dispersal of *Rhopalurus rochai* offspring from wild-caught pregnant females maintained in the laboratory.

Number of individuals/ litter	Interval between birth and 1st molt (days)	Dispersal time (days)	Survival ratio of 1st and 2 nd molts (%)
34	9	2–9	100
29	8	3–5	100
55	7	2–8	100
23	10	1–6	100
38	8	2–4	100

and to determine litter size, interval between birth and 1st ecdysis, dispersal time and number of individuals that molted into the 2nd instar. Because the offspring clustered on the female dorsum making an exact count very difficult, litter size was considered as the total number of individuals recorded after dispersal. Every living and dead individual was counted except for those that were cannibalized by the female.

The relation between feeding and molting was studied in a group of 38 juveniles in the 2nd instar that were obtained from the litters of two females. Just after dispersal, scorpions were weighed and divided into three groups: not fed (n = 10); fed once/week (n = 13); fed three times/ week (n = 15). In each group, scorpions were weighed before and after feeding, including those that did not feed. One prey item (1st instar nymph of *P. americana,* approximately 5.50 ± 0.90 mg) was fed to each juvenile each time. The difference between final mass and initial mass was used to determine the influence of feeding on molting success, survival and intermolt period in these groups. Juveniles from the unfed group were weighed at the beginning of the experiment and after death.

The biomass growth of scorpions fed once and three times per week was compared using a Student's t test and the mortality of the two groups was evaluated using a χ^2 test. Correlations between initial biomass and intermolt period, as well as between initial biomass and life span of the food-deprived individuals, were tested using Spearman correlation because the data were not normally distributed. The normality and variance homogeneity of the data were tested using Shapiro-Wilk and Levene tests, respectively. All tests were conducted with STATISTICA 7 software with a significance level 0.05. Voucher specimens are deposited at the Entomological Collection of the Laboratory of Terrestrial Invertebrates, Universidade Federal de Pernambuco, Brazil. Most specimens were alive at the time this manuscript was completed, and they will be deposited at the same place as soon as they die.

RESULTS

Litter size.—The average number of recorded offspring in *R. rochia* was 35.8 ± 12.11 individuals (range = 23–55) (Table 1). Cannibalism by the female was recorded only at the moment of birth in four out of the five observations. It was not possible to determine the number of cannibalized stillborns due to the difficulty of viewing the act once the offspring were hidden by the pedipalps. However, it was possible to observe that the cannibalized offspring showed a highly softened, sometimes wrinkled tegument and small size when compared to those on the dorsum.

First instar duration and dispersal time.—Litter size, 1st instar duration, survival, and dispersal of *R. rochai* offspring are shown in Table 1. The first molt was assessed in 179 individuals from different litters and occurred on average 9 days after birth (range = 7–10 days) and occurred on the same day in all individuals from the same brood. Dispersal started 1–3 days after the 1st molt and was completed 4–9 days after that. Occasionally, juveniles were observed to climb down from the mother's back. No dead scorpions were found during the 1st instar period, and all juveniles reached the first molt.

Effects of starvation and feeding on body mass and molting.—Mean mass variation, intermolt period, and molt frequency of *R. rochai* under different feeding treatments and mass variation during starvation are shown in Table 2. Overall mean body mass just after juveniles climbed down from their mother's dorsum was on average 16.43 ± 1.28 mg (ranging = 12.3–18.7 mg). The initial biomass was not correlated with total life span in food-deprived animals (r = 0.18, P = 0.61) (Fig. 1A). Among these individuals, none (n = 10) reached the 2nd molt, with mortality occurring between 11 and 30 days after the 1st ecdysis. The biomass lost during food deprivation was on average 2.8 mg (range = 2–4 mg) with the lowest mass of 10.5 mg and highest 14.7 mg. No relationship was observed between initial biomass and weight loss. Feeding more often did not influence molting success but did extend the intermolt period (fed once per week: r = −0.34, P = 0.36, and fed three times per week: r = 0.59, P = 0.04) (Fig. 1B, C). The scorpions fed three times per week showed a greater biomass increase (53.0 ± 13.2 mg) when compared to those fed only once (45.0 ± 4.1 mg), though this difference was not significant (t = −1.73, df = 16, P = 0.10) (Fig. 1D). In the group fed once per week, the minimum weight for molting was 39.6 mg and the maximum was 51.8 mg, while in the other group the minimum was 34.3 mg and the maximum was 79.9 mg.

Mortality was 30.8% (n = 4/13) among those fed once per week and 40.0% (n = 6/15) among those fed three times per week. No significant difference was found in mortality between groups fed once or three times per week (χ^2 = 0.18; df = 1; P = 0.67). In the former group, 100% of the deaths occurred during intermolt, while in the latter 20% were recorded during ecdysis. The mean intermolt period increased 22.48 days in the group fed more often, varying from 169.77 ± 28.97 days in the group fed only once per week to 192.25 ± 44.60 days in the group fed three times per week (Table 2).

DISCUSSION

Most reproductive traits, such as litter size, 1st instar duration, dispersal time, and survivorship show a large variation among scorpion species (Polis & Sissom 1990). Average litter size of *R. rochai* recorded in this study (approximately 36 young) is one of the largest brood sizes yet described for buthid scorpions. Females from most buthid species give birth to fewer than 27 young (see summary by Lourenço 2002). A previous study (Matthiesen in Polis & Sissom 1990) has described litter size having range = 28–49 individuals in *R. rochai.* The difference in the number of offspring relative to our findings (23–55 young) may indicate adaptation to microvariation in

Table 2.—Mass variation, intermolt period and molt frequency of *Rophalurus rochai* during starvation and different feeding patterns. Final mass for starved juveniles was considered by weighing individuals after death. For other groups, final mass = offspring mass before molt or at death during molt.

Feeding regime	Initial Mass (mg)	Final Mass (mg)	Mass lost during molt (mg)	Molt frequency (%)	Molt interval (days)
Starvation (n = 10)	15.04 ± 1.36	12.60 ± 1.28	-	-	-
Feeding once (n = 13)	17.00 ± 1.04	45.01 ± 4.14	7.7 ± 4.36	69.2	169.77 ± 28.97
Feeding three times (n = 15)	17.03 ± 0.99	53.04 ± 13.56	3.44 ± 3.46	60.0	192.25 ± 44.60

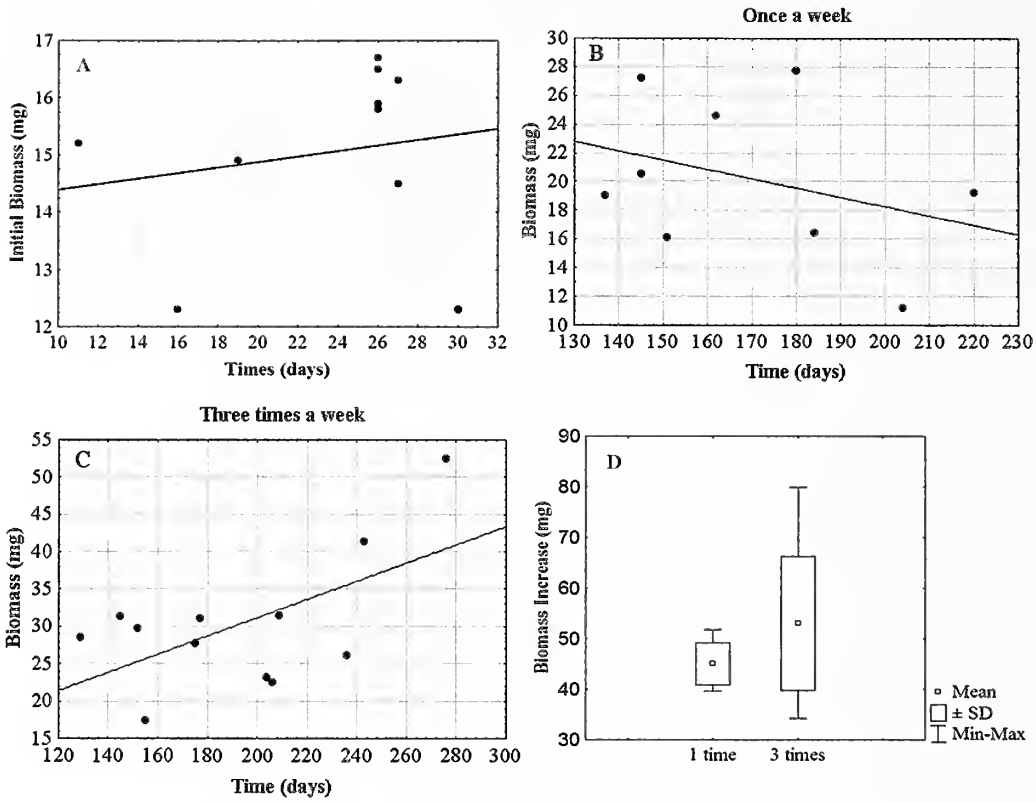

Figure 1.—Aspects of post-embryonic development of 2nd instar *Rhopalurus rochai*. A. Correlation between initial biomass and total life span in food deprived juveniles. B, C. Intermolt period as a function of feeding frequency: B. Once a week; C. Three times/week. D. Relative biomass increase in the scorpions fed once or three times a week.

the environment faced by females from the different populations used in the two studies and also may reflect genetic differences among populations as suggested by Brown & Formanowicz (1995). The number of 2nd instars (just after dispersal) in broods of *R. rochai* also represented a wide range (23–55). Such variation may be partly influenced by differences in female mass or cannibalism, as observed by Warburg & Elias (1998) for the large number of 1st instars in the litter size (17–33) recorded in *Scorpio maurus fuscus*. Among female scorpions, cannibalism of newborns is a normal behavior that makes estimation of offspring numbers more difficult (Polis 1980). In this study, cannibalism was observed during parturition in 80% of pregnant females.

Like all scorpions (Williams 1969; Lourenço 1979a, b, 1991; Polis & Sissom 1990), females of *R. rochai* provide maternal care to offspring for several days after giving birth to live young. During this 1st instar phase, the young remain on their mother's back without feeding, and this may be considered a continuation and extension of embryological development (Farley 2005). In general, the duration of this period ranges from 5 to 25 days (Lourenço 2002). In this context, *R. rochai* showed a short 1st instar phase (8 days) which was similar to *Centruroides gracilis* (Latreille 1804) (8 days) (Francke & Jones 1982) and *Centruroides exilicauda* (Wood 1863) (7 days) (Brown 2004) and half as long as *Tityus trivittatus* Kraepelin 1898 at 16 days (Toscano-Gadea 2004).

Although feeding success can be considered a measure of individual fitness, the rate of food intake among juvenile scorpions under natural conditions is still largely unknown. Food supplementation in *R. rochai* did not increase the chances of molting, but significatively extended the intermolt period. In addition a tendency toward increased mortality was also observed in this group. Similarly, *Nephila clavipes* (L. 1767) spiders were more likely to die at or immediately before the next molting cycle after getting larger quantities of food, indicating a possible physiological cost of rapidly increasing mass (Higgins & Rankin 2001). Therefore, when prey is abundant, it may represent a real cost to the development of opportunistic feeders such as spiders and scorpions.

The increasing mortality risk due to intake of a large number of prey is known in other invertebrates. Survival of *Aedes aegypti* larvae was reported to be lower at the highest feeding levels when immature specimens were reared in the laboratory (Arrivillaga & Barrera 2004). Scorpions are predators of small arthropods and may feed infrequently during their life, which may last many years (Lighton et al. 2001). Hence the ability of immatures to survive at low feeding rates is a considerable adaptation for facing periods of low prey availability.

The 2nd instar duration for *R. rochai* fed weekly was on average 170 days. Starved individuals in the same instar survived 30 days maximum (initial weight = 16.43 ± 1.28 mg), indicating the low resistance of these invertebrates to lack of food. In contrast, according to Tanaka & Itô (1982) and Rickers & Scheu (2005), spiders are tolerant to starvation for a long period of time. In a common grasslands spider, *Pardosa palustris* (L. 1758), for instance, the second instar juveniles with the initial weight of 0.32 ± 0.07 mg survived 9.86 ± 2.28 days in starvation (Rickers & Scheu 2005). In the wolf spider, *P. astrigera* (L. Koch 1878), adult males and females could survive on average 28.8 ± 2.7 days and 54.4 ± 18.9 days, respectively, without any food (Tanaka & Itô 1982).

Relative to other developmental phases, the 2nd instar of *R. rochai* must be a critical period for growth because the previous instar juveniles do not feed and must expend all of their nutritional reserves for molting and survival. In the scorpion *Pandinus imperator* (C.L. Koch 1841), for instance, weight at birth is 443 mg and decreases to 381 mg after the first molt (Mahsberg 2001). Nutritional reserves at the start of the 2nd instar in *R. rochai* are likely to be the lowest of the entire life span and successful foraging is crucial to survival. Reduction in body weight due to starvation up to death was on

average 13.3% of the starting weight. In other arthropods such as the spider *Pardosa palustris*, starving second instar juveniles with an initial weight of 0.32 ± 0.07 mg survived 9.86 ± 2.28 days (Rickers & Scheu 2005). Lower tolerance to starvation was described for the juvenile Chinese mitten-handed crab (*Eriocheir sinensis*) which survived over 70 days (initial weight = 4.01 mg) (Wen et al. 2006).

The physiological cost of food supplementation with a rapid increase in mass in *R. rochai* is unknown but appears to have a fundamental effect on population dynamics by prolonging the time for a new generation to be formed.

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SHORT COMMUNICATION

Courtship and mating behavior of *Grammostola schulzei* (Schmidt 1994) (Araneae, Theraphosidae), a burrowing tarantula from Argentina

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Abstract. *Grammostola schulzei* (Schmidt 1994) comprises a medium-bodied tarantula. Recently the species was found in Sierra de la Ventana, Buenos Aires, Argentina, where it lives in burrows always made under stones in rocky hills. Our objective was to offer a detailed description of courtship and mating, heretofore unknown, and to determine, under laboratory conditions, where copulation takes place: in the open field as proposed for all species of *Grammostola*, or at the entrance of the burrow. We carried out two series of experiments, completing 40 trials (20 in open arenas and 20 in burrowing arenas). All males initiated sexual behavior after contact with female silk. Courtship involved palpation, palpal drumming, body vibrations, and leg tapping. Palpation and palpal drumming appeared to operate in different ways. Females displayed typical behavior of a burrowing tarantula, making rapid bouts of tapping vigorously with the first pair of legs and palps. The mating position observed was typical of mygalomorphs, in which the female raises her body up and opens her fangs, the male uses the tibial apophyses to clasp the female's fangs, and finally begins a series of attempts at palpal insertion. The smooth slapping during clasping may serve to keep the female passive and relaxed. The dorsal flexion observed during mating and the number of successful matings in open arenas suggests that copulation would take place outside the burrow. We observed sexual cannibalism during the interactions but in these cases, we registered no previous courtships by the males.

Keywords: Theraphosinae, sexual display, copulation, female response

Resumen. *Grammostola schulzei* (Schmidt 1994) es una tarántula de tamaño medio. Recientemente la especie se colectó en Sierra de la Ventana, Buenos Aires, Argentina, donde vive en cuevas hechas siempre bajo piedras en cerros rocosos. Nuestro objetivo fue ofrecer una descripción detallada del cortejo y apareamiento y poner a prueba bajo condiciones de laboratorio dónde tiene lugar la cópula. Se realizaron dos series de experimentos completando 40 en total (20 en arena abierta y 20 en arena con cueva). Todos los machos iniciaron el comportamiento sexual luego de contactar con la seda de la hembra. El cortejo involucró movimientos de palpar, golpeteos de palpos, vibraciones corporales y golpes con el primer par de patas. Las secuencias de palpar y golpeteos de palpos parecen actuar de maneras distintas. Las hembras mostraron un comportamiento típico de tarántulas que habitan cuevas, realizando golpeteos rápidos con el primer par de patas y palpos. La posición de cópula observada fue similar a la de otras migalomorfas, en la cual, la hembra eleva su cuerpo y abre los quelíceros, el macho utiliza sus apófisis tibiales para engancharlos y por último comenzar una serie de inserciones palpales. Los golpes suaves durante el enganche servirían para mantener una condición pasiva y relajada de la hembra. La flexión dorsal observada durante la cópula y el número de cópulas exitosas en arena abierta sugiere que el apareamiento tendría lugar fuera de la cueva. Hemos observado canibalismo sexual durante las interacciones, pero en estos casos no hubo cortejo previo de los machos.

Few studies have been conducted on the reproductive behavior of tarantulas in general (Baerg 1958; Minch 1979), and the small amount of published literature that contains detailed behavioral descriptions (Shillington & Verrel 1997; Jackson & Pollard 1990) suggests that the traditional portrayal of mygalomorph display behavior as "simple" (Platnick 1971; Foelix 1996) is misleading. Moreover, an understanding of tarantula reproduction is necessary to facilitate captive breeding and to reduce pressures on wild populations caused mainly by human impact and pet commerce (Costa & Pérez-Miles 2002). The South American genus *Grammostola* Simon 1892 (Bücherl 1951). includes large-sized species whose carapace length varies from 20–30 mm (Postiglioni & Costa 2006). The great density and diversity of specimens of *Grammostola* spp. in Argentina has led researchers to think that Argentina is the dispersion center of the genus. In Argentina, it has a different biotope than Brazilian species (Schiapelli & Gerschman 1960). Bücherl (1951) described the reproductive biology of several species of *Grammostola* but only for medical or systematic purposes. Recently, two allopatric species living in Uruguay have received a considerable amount of attention regarding their reproductive biology: *Grammostola iheringi* (Keyserling 1891), which has been reported only from neighboring areas of Quebrada de los Cuervos, and *G. mollicoma* (Ausserer 1875) which is widely distributed throughout the country (Pérez-Miles & Costa 1992; Costa & Pérez-Miles 2002; Postiglioni & Costa 2006).

Grammostola schulzei (Schmidt 1994), is a burrowing species from Argentina whose males are much smaller than females (Males are 30 mm long) (Schmidt 2005). Bertani & Fukushima (2004) identified specimens from Cordillera de Los Andes (Argentina), Tandil (Buenos Aires, Argentina), and the species was also collected in Sierra de la Ventana (Buenos Aires, Argentina), where it lives in burrows made under stones in rocky hills (Ferretti & Ferrero 2006).

In this paper we offer a detailed description of courtship and mating under laboratory conditions. We provided two different types of arenas for the matings to occur: an open area similar to an open field as proposed by Costa & Pérez-Miles (2002) for all species of *Grammostola*, or at the entrance of the burrow.

METHODS

Spiders.—Five males and eight females of *G. schulzei* were collected by hand during the summer of 2006 in the locality of Sierra de la Ventana, Buenos Aires, Argentina (38°07′63″S, 61°47′30″W); and the observations were made during the November–December period of 2006. Due to cannibalism, we needed to capture three more males to maintain the number of five individuals to obtain the data. Voueher specimens were deposited in the Entomological Colleetion of Zoology of Invertebrates II, Universidad Nacional Del Sur, Buenos Aires, Argentina. All the females molted in the laboratory between January and February of 2006 so they had no stored sperm. Individuals were raised in glass vials of 13 cm diameter or glass rectangular cages of 30 × 14 cm according to their size. They had a substrate of soil, water provision, and were fed *ad libitum* with coekroaches (*Blattela germaniea*) and *Tenebrio* sp. larvae (Coleoptera). The average environmental temperature was 26.7° ± 1.52° C.

We carried out two series of pairings in cages measuring 30 × 35 and 30 cm high and completed 40 trials (20 each). The first series was performed in conditions with a layer of soil of approximately 2 cm deep, which we called an "*open arena.*" In the second series, the layer of soil was 10 em deep and a burrow was excavated against the glass wall allowing for observation. This constituted the "*burrowing arena.*" This burrow simulates natural conditions and was recommended for experiments (Postiglioni & Costa 2006). In both situations, the female was plaeed in the eage at least 24 h before trials to permit pheromone deposition with silk on the soil surface. The individuals in a pair were never tested together more than once and none was used in more than one test on a given day. Each pair of spiders was reused at least 1 day after the first experiment, but in different combinations. Individuals were randomly assigned to pairs and experimental series.

The observations began by carefully depositing the male far from the burrow entrance (*burrowing arena*) or the female's position (*open arena*) and ended after a 60 min period of non activity or when the copulation concluded.

Description and analysis.—Eneounters were recorded by direct observations, notes, and videotape (85% of encounters) with a Sony Cyber-Shot DSC-H2 (60 fps). Video records were analyzed using the PC program Video edit magic 4.23 in order to accurately describe behavioral patterns, using slow motion and single frame advance modes. Normality and homogeneity of variance of continuous variables (durations of the behaviors) were tested using the Kolgomorov-Smirnov and Levene tests respectively. Parametric Student's *t*-test (non-paired samples) was used for parametric durations. Non-parametric Mann-Whitney *U*-test (non-paired) for frequencies and Kolgomorov-Smirnov two sample tests were used for non- parametric durations. All statistical analyses were performed using SPSS version 14.0 for Windows (2005). Averages are given ± 1 standard deviation.

RESULTS

We recorded a total of 13 successful matings during 40 trials, 9 in the *open arena* and only 4 in the *burrowing arena*. All courtship behaviors were initiated by males after contact with female silk. In the unsuccessful courtships (27 in all encounters) where the copulation failed, all involved unreceptive females either did not offer any signal or attacked the males.

Courtship behavior.—Duration of courtship was of 18.98 ± 13.82 min, and in 77% of the cases courtship started with male "palpating," a behavior which consisted of the two palps moving up and down in an alternating manner, hitting the soil with a constant velocity. Bouts of palpating were highly variable in duration (8.15 ± 5.93 s, range = 1.15–21.26 s) and were always performed at > 20 cm from the female. "Palpal drumming" was also common and started at low velocity (4.5 ± 1.73 bouts/s), frequency of 3 Hz, and increased sequentially (12.5 ± 2.08 bouts/s), frequency of 13 Hz. The duration of a bout of palpal drumming was 6.27 ± 1.39 s and was more conspicuous after any movement by the female or near her (~ 10 cm). It often interrupted the bouts of palpation. When comparing mean durations of male signaling bouts (palpation and palpal drumming), no significant differences were found (non-paired *t*-test, $t = 1.69$, $P > 0.05$). In all cases with palpal drumming, the male displayed body vibrations caused by the movements of legs III and could not be quantitatively described using the video because it was not possible to observe male movements in detail. Leg tapping involved only legs I and consisted in elevating a leg, extending it, and lowering it rapidly to hit the soil. The pattern could include each leg independently or simultaneously and was always observed in conjunction with palpating. During courtship, the sequence of palpation, palpal drumming, vibration, leg tapping was more frequent. The frequency of these bouts in *open* and *burrowing arenas* are given in Table 1. We observed males laying down silk over the female's silk strands in 21 interactions (3.09 ± 2.58 bouts/interaction) during courtships.

One female (*open arena*) made rapid bouts of tapping vigorously at low amplitude with the first pair of legs and palps by flexing, lifting and lowering against the substrate. This was carried out seven times after the third palpal drumming by the male and he reoriented towards the female. No statistical differences were found using the Mann-Whitney test either when comparing the frequency of bouts of palpation in *open arena* and *burrowing arena* ($U = 141.5$, $P > 0.05$), or when comparing the frequency of bouts of palpal drumming in *open arena* and *burrowing arena* ($U = 160.5$, $P > 0.05$).

Copulation.—For mating, the male started to display spasmodic "beats" that involved only the second pair of legs that vigorously hit the body of the female during clasping and unclasping. The pattern for this could be alternate or synchronous. We observed a total of 226 bouts (16.14 ± 10.20 bouts per copulation). The female performed "gaping display" in whieh she raised her carapace, extended the two first pairs of legs, and also opened her fangs. Typically, when the female did this behavior, the male lunged toward the female and clasped her chelicerae with the tibial apophyses. After this, the male pushed up the female's body, raising her to reach a position that formed an angle of 60–80° between carapace and abdomen and the female entered a passive state, becoming quiescent. During clasping, the male sometimes displayed smooth slapping over the female's carapace by the metatarsus and tarsus of legs II. This was in either alternate or synchronous form.

Finally the male began a series of palpal insertion attempts. The number of insertions per copulation was 4.23 ± 3.70 SD. The

Table 1.—Behavioral units performed by five males of *Grammostola schulzei* during courtship in *open arena* and *burrowing arena*. *n* = total number of courtships where the behavioral unit took place; the mean is the number of bouts per courtship of all males.

	Open arena			*Burrowing arena*		
Behavioral units	Mean	SD	*n*	Mean	SD	*n*
Palpate	13.46	13.27	15	17.22	21.93	9
Body vibrations	6.91	8.10	12	9.87	7.88	8
Palpal drumming	10.25	14.06	16	17.40	19.72	10
Leg tapping (one leg)	18.28	42.59	14	27.00	15.72	4

duration of copulation was 204.52 ± 183.13 s. When a female was inside the burrow, we observed two copulations at the burrow entrance and two outside the burrow at a distance of approximately 10 cm. No statistical difference was found when comparing duration of copulation between *open arena* and *burrowing arena* using the Kolmogorov-Smirnov test (non-paired, $Z = 1.10$, P 0.05). We recorded three cases of sexual cannibalism in which the female attacked and killed the male before mating, one case in *open arena* and two in *burrowing arena*. Also we observed two attacks by females against males before mating, but they were able to escape with a series of injuries.

DISCUSSION

Courtship behavior.—Early work on mygalomorphs proposed that mygalomorphs lacked chemical cues in sexual communication (Baerg 1958; Platnick 1971); however, our results agree with more recent studies that confirm the existence of female contact sex pheromones (Minch 1979; Prentice 1997; Shillington & Verrell 1997; Yañez et al. 1999; Costa & Pérez-Miles 2002). Palpation occurs at a greater distance than palpal drumming and generally initiates the courtship; palpal drumming may serve as a short-distance communication mechanism near the burrow entrance (Pérez-Miles et al. 2007). These behaviors were considered the same behaviors that, in other studies, were referred to as palpal drumming (Costa & Pérez-Miles 1992; Shillington & Verrell 1997; Yañez et al. 1999; Quirici & Costa 2005), but in *G. schulzei* they seem to operate in different ways because, after a response from the female, the male only engages in palpal drumming and stops palpating. Although we found no differences in duration of these bouts, the frequency (Hz) and velocity are different. Palpation could be similar to the behavior described for other mygalomorphs (Jackson & Pollard 1990). Body vibration is a widespread behavior in the courtship of Theraphosidae (Minch 1979; Prentice 1997; Costa & Pérez-Miles 2002) and is very common in *Acanthoscurria suina* Pocock 1903 and *Eupalaestrus weijenberghi* (Thorell 1894), two burrowing tarantulas (Quirici & Costa 2005; Pérez-Miles et al. 2007). In *G. schulzei* body vibration always occurs in synchrony with palpal drumming and this is not the case for other species of *Grammostola* (Pérez-Miles & Costa 1992; Postiglioni & Costa 2006). Leg tapping had been described by Baerg (1958), Prentice (1997) and Shillington & Verrell (1997) for *Aphonopelma* spp. males and for *G. mollicoma* and *G. iheringi* by Postiglioni & Costa (2006), indicating that this behavior could be acting as a series of communicatory signals in sexual context, maybe using a seismic and/or acoustic channel. We observed leg tapping far away from the female's position acting as primary signals; moreover, this species displays leg tapping only with the first pair of legs.

The laying down of silk by males was also reported for *Brachypelma klassi* (Schmidt & Krause 1994) (Yañez et al. 1999) and these authors suggest that it may be a method of interfering with chemical or tactile cues that may be used by subsequent males to locate the female. However, our results showed that the males had no trouble finding the female's position and mate successfully.

The leg tapping displayed by the female had not been observed in other species of *Grammostola* and is described here for the first time. Coyle (1986) observed a similar behavior in a Dipluridae. In Theraphosidae, it was first observed by Prentice (1992) for three species of *Aphonopelma*. Quirici & Costa (2005) found that both *E. weijenberghi* and *A. suina* respond to male courtship from inside their burrows suggesting that such action would not only inform the male about her willingness to copulate, but also help the male orient himself towards the burrow entrance.

Curiously, this behavior was performed by one female in *open arena* and the male reoriented himself towards the female, suggesting that this behavior, at least in *G. schulzei*, seems to be important for orientation rather than indicating the receptive state of the female because we obtained more successful matings with females that did not respond. Moreover, the male who elicited this response from a female had an unusual additional thorn spine on the internal tibial apophyses, and this deformity could have generated novel signals maybe in leg tapping as was observed for body vibrations in *E. weijenberghi* (Pérez-Miles et al. 2007).

Copulation.—The male's spasmodic beating with legs II is unique to *Grammostola* and could be a synapomorphy for this genus (Costa & Pérez-Miles 2002). These authors also suggest that its function could be to relax the female's fangs, taking into account that it is mainly displayed during clasping and unclasping. The mating position observed in the present study was typical of mygalomorphs (Coyle & OShields 1990). The dorsal flexion observed implies that the copulation would take place outside the burrow. Moreover, we obtained more successful matings in the open field than at the burrow entrance without any problem of equilibrium, but the low number of successful matings in the *burrowing arena* could be attributed to the absence of the female's silk in some interactions. This raises the question of why the female shows a characteristic behavior of a burrowing tarantula that "pledges" the species to strictly copulate at the burrow entrance. This mating system was proposed for the burrowing tarantulas (Costa & Pérez-Miles 1992; Shillington & Verrell 1997; Yañez et al. 1999; Pérez-Miles et al. 2007) and seems to be inconsistent with our results, but this needs to be elucidated with more data.

The smooth slapping was not observed for other theraphosids and is reported here for this species. This behavior may serve the same function as palpal boxing in *Brachypelma klassi*: to maintain the female's "passive" state (Yañez et al. 1999).

The number of insertions was similar to that reported for other species of Theraphosidae (Baerg 1958; Minch 1979; Pérez-Miles & Costa 1992) but the copulation duration was brief (lasting only a few minutes) in relation to other species of *Grammostola* (Pérez-Miles & Costa 1992). This could minimize the predation risk of the couple in an exposed mating site (Punzo & Henderson 1999). We observed sexual cannibalism, but its absence seems to be the rule for theraphosids (Costa & Pérez-Miles 2002). However, even a low frequency of cannibalism may be a significant problem for males, a problem solved by courtship (Jackson & Pollard 1990). In fact, in all the cases in which the females attacked and killed or injured males, we registered no previous courtships by the males.

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